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MORPHOLOGY AND HOMOLOGOUS FEATURES IN THE MALE PALPAL ORGAN IN PISAURIDAE AND OTHER SPIDER FAMILIES, WITH NOTES ON THE TAXONOMY OF PISAURIDAE (ARACHNIDA: ARANEAE)

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> "The question as to whether the genitalic characters on which this subfamily [Otiothopinae; Araneae, Palpimanidae] is based are primitive or derived cannot be answered with certainty. Although it is often comparatively easy to make this decision regarding somatic characters in spiders, the opposite is generally true for genitalic characters. Our understanding of the evolution of spider genitalia is extremely limited, because of the astounding diversity of structures . . . "
>
> N. I. Platnick (1975: 2)

ABSTRACT. A detailed morphology of the male copulatory organs, the genital bulb, in *Architis, Charminus, Dolomedes, Paradossenus, Pisaura, Pisaurina, Staberius, Thaumasia* and *Trechalea* is presented. The homology of several palpal elements within the Pisauridae is established; possible homology with those in various other spider families is discussed. Homology concepts concerning the median apophysis, the conductor, and the spiral embolus are discussed. The character states are evaluated and polarized. The groundplan of the pisaurid genital bulb is compared with the bulb in Mesothelae. An update on the systematics of the family Pisauridae is presented and systematic implications from the analysis of the male copulatory organs are discussed. Two large monophyletic genus-groups, a mainly African *Pisaura* genus-group including about 20 genera, and a *Trechalea* genus-group comprising eleven South American genera, are recognized. *Paradossenus taczanowskii* Caporiacco, 1948, is a junior synonym of *P. nigricans* F. O. Pickard-Cambridge, 1903. The validity of two nominal genera, *Architis* and *Staberius*, is discussed. The genera are likely to be synonymous. The structure of the egg sacs of *Syntrechalea, Dyrines* and *Hesydrus* are described for the first time.

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INTRODUCTION

The copulatory organs in male spiders are located at the distal segment of their pedipalps. They are secondary organs serving the transfer of sperm. They are not connected to the testes but have to be charged prior to copulation. The male copulatory organs form a highly complex morphological structure, the genital bulb. It functions hydraulically and is composed of inflatable membranes (hematodochae) and larger sclerites (subtegulum and tegulum). Additionally, projections and processes, often called apophyses, are attached to various parts of the palp. Inside the genital bulb lies the sperm duct that serves as a storage place for sperm. The sperm duct opens at the tip of the embolus, an intromittant organ. During copulation, the embolus is partly or totally inserted in the female epigynum to transfer sperm.

The male genital bulbs are diverse in structure and in most cases species-typical. They have been used for species identification since the study of male sexual organs started with the works by Westring (1861), Blackwall (1843) and Menge (1843, 1866-1879). An important work on details of their morphology was published by Comstock (1910). He studied unexpanded and expanded bulbs of different spider groups and introduced a nomenclature of hematodochae, sclerites and apophyses that is still used today. There are numerous taxonomic monographs that illustrate male (and female) copulatory organs. But accurate labelling of those figures is rare. Often, Comstock's nomenclature is applied uncritically, with the result that homology of sclerites is inevitably implied but seldom discussed. Since homology of many elements in the male genital bulbs has never been clearly established, the use of these organs for phylogenetic reconstruction is hampered.

The theme of this paper arose from a study on the systematics of the spider family Pisauridae. The systematics of the Pisauridae is unsatisfactorily resolved. The sister group is unknown, the superfamilial position is in dispute, and currently used subdivisions within the family are not monophyletic. In this study, characters of the male copulatory organs will be analyzed to clarify systematic problems of Pisauridae.

In this endeavor, there are two main obstacles. First, the structures of male genital bulbs of Pisauridae are poorly known. Roewer's (1955) drawings and labelling are not accurate enough to reveal the morphology of the genital bulb in African pisaurid genera he revised and are useless for systematic and phylogenetic conclusions. Blandin's (1974–1979) work on African and Carico's (1972–1981) work on American Pisauridae provide better insight into the morphology of palps of particular genera. However, male organs were rarely studied in their expanded form. Therefore, the serial relationships of palpal sclerites and apophyses are mostly unknown. Secondly, morphological features found in genital bulbs have to be evaluated regarding the question of homology. Only homologous characters with their character states furnish data for a cladistic analysis. The main objective of the present study is the definition of homologous structures and homologous sectors of the male genital bulb within Pisauridae and to discuss some aspects of homology of palpal structures in Araneae in general.

Although the male copulatory organs in spiders show, as Eberhard (1985) discussed, rapid and divergent evolution, the morphological groundplan of palps appears to be unexpectedly old. In the third part of the DISCUSSION some rather provocative (and speculative) hypotheses concerning the homology of embolus, median apophysis and conductor are presented. Homology concepts are discussed in the light of other such hypotheses put forward by Kraus (1978), Haupt (1983), Raven (1985) and Coddington [in press].

MATERIALS AND METHODS

Genital bulbs of the following species were studied (locality and collection included):

Architis cymatilis Carico, 1981. ♂ preserved with expanded palp [Peru: Madre de Dios, Zona Reservada Pakitza (11°58'S, 71°18'W); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MHNSM), Lima, Peru].

Architis tenuis Simon, 1898 [Brazil: Mato Grosso, Vila Vera, Oct. 1973; American Museum of Natural History (AMNH), New York. Colombia: Mata, Puerto Lopez; Museum of Comparative Zoology (MCZ), Cambridge, USA].

Charminus camerunensis Thorell, 1899 [Cameron: Kitta; syntypes; Naturhistoriska Riksmuseet (NHR), Stockholm].

Dyrines striatipes (Simon, 1898) [Peru: Madre de Dios, Zona Reservada de Manu, Puesto de Vigil. Pakitza, quebrada El Bano (11°58'S, 71°18'W) 5.X.1987; National Museum of Natural History (USNM), Washington, DC. ♀ with egg sac; Peru: Amazonas, alto Rio Comaina, Puesto de Vigilancia, 850-1150m; MHNSM].

Dolomedes scriptus Hentz, 1845 [USA: Virginia, Lynchburg, April 1985; USNM].

D. tenebrosus Hentz, 1843 [USA: Washington, DC; USA: Virginia, Lynchburg, April/May 1985; USNM].

D. triton (Walckenaer, 1837) [USA: Virginia, Lynchburg; USNM].

Enna O. Pickard-Cambridge, 1897, unidentified species [Bolivia: USNM. Peru: Piura, Rio Mangas, 1500m; MHNSM].

Hesydrus Simon, 1898, unidentified species [Peru: Amazon, Cordillere del Condor, alto Rio Comaina, Puzz, Falso Paynisha, November 1987; MHNSM. ♀ with egg sac; Venezuela: Muséum Nationale d'Histoire Naturelle, Paris (MNHN) Boc 2042, Boc 2043, Boc 2044].

Paradossenus nigricans F. O. Pickard-Cambridge, 1903 [Guyana: Two Mouths, Essequibo River; Museo Zoologico della Specola (MZS), Firenze, Italy. Guyana: Tibicuri-Cuyaha, Demerara River; Caporiacco's specimens, type of *P. tascanowskii* Caporiacco, 1948; MZS].

Pisaura mirabilis (Clerck, 1758) [Austria: Tirol, Innsbruck, June 1964; USNM].

Pisaurina mira (Walckenaer, 1837) [USA: Virginia, Lynchburg; USNM. USA: New York, Bear Mt., May 1947; AMNH].

Staberius spinipes (Taczanowski, 1873) [Peru: Pucallpa, Nov. 1946; AMNH].

Syntrechalea F. O. Pickard-Cambridge, 1902, unidentified species. ♀ with egg sac [Peru: Cusco, Atacaya; MHNSM].

Syntrechalea porschi Reimoser, 1939 [Costa Rica: Limón, Hamburg Farm; Naturhistorisches Museum, Wien, Austria (NHMW)].

Thaumasia cf. *uncata* F. O. Pickard-Cambridge, 1901 [South America, country unknown, "San Esteban"; MNHN Boc. 2047b, No. 11750. Mexico: Veracruz (95°07'W, 18°36'N); MCZ]. Carico (1981: 150) states that *Thaumasia argenteonotatus* (Simon, 1898) is a senior synonym of *Thaumasia uncata*.

Thaumasia cf. *velox* Simon, 1898 [Colombia(?): "Col. Alpine"; MNHN, Boc. 2047b, No. 19190. Ecuador: Morona-Santiago, Sucúa, 1000m, June/July 1979, N. Engler; MCZ].

Tinus peregrinus (Bishop, 1924) [Mexico: Nuevo Leon, Linares, July 1956; AMNH].

Thalassius spinosissmus (Karsch, 1879) [South Africa: Natal, Pietermaritzburg; USNM].

Trechalea Thorell, 1870, unidentified species [Venezuela: Miranda, Guatopo, National Park Santa Cruzita, 450m, J. Coddington; USNM].

Expansion of genital bulbs

Palps were submerged overnight in a weak watery solution of potassium hydroxide (KOH), in which they expanded to varying degrees. They were then transferred to distilled water, where further inflation occurred. The structure of unexpanded bulbs was studied by submerging them in Hoyer's mounting medium for the time of observation. They became partly translucent. The drawings were made with aid of a dissecting microscope with drawing tube.

Homology

Classical criteria were applied to reach decisions on the homologous status of features: (a) criterion of position, (b) criterion of special, morphological similarity, and (c) criterion of concordance with other characters (Remane, 1952; Wiley, 1981: 130-138; Patterson, 1982). To allow comparison of the positions of apophyses on the tegulum in different genera, the terms proximal and distal are used as defined below in order to accommodate criterion (a).

Terms

Differing from common usage, the terms proximal and distal in the tegulum here refer to the position of a particular part in relation to the trajectory of the sperm duct. Following the course of the sperm duct, starting at the fundus, apophyses inserting on the tegulum near the fundus are considered proximally located. Apophyses inserting closer to the ejaculatory duct are referred to as being distal. The terms dorsal and ventral refer to the position of a particular part within the depth of the genital bulb. Parts nearest to the dorsal surface of the cymbium are located dorsally; ventrally located parts are mostly visible in the unexpanded bulb in ventral view (as they are figured here).

In descriptions of pisaurid palps, the terms median apophysis and conductor are used to name tegular apophyses that are proposed to be homologous within (at least) all Pisauridae. The term terminal apophysis is used for any apophysis of the apical division; thus homology among different pisaurid genera is not implied.

The term homologous refers to the actual structures (= character, e.g., conductor) that are proposed to be based on an identical evolutionary event. The particular structure may appear in several character states. Similar character states of a character in several taxa may be based on the same evolutionary event, thus the character state in question is considered homologous and representing a synapomorphy. Apparently similar character states of one character based on different evolutionary events have to be considered homoplasous, and thus do not indicate phylogenetic relationship (*see* Patterson, 1982: 25).

Text conventions

All statements of positions of sclerites refer to the unexpanded left bulb in ventral view, unless indicated otherwise.

All references to figures presented in this paper are made using the abbreviation "Fig."; references to figures in other publications are abbreviated as "fig." Terms used by other authors to describe parts of the male copulatory organs are added in parentheses to facilitate finding the cited text.

Abbreviations (including terms of authors)

ad I, II, III bulbous sections of the apical division in *Pisaurina*
an anelli of the subtegulum
bmt basal membraneous tube of apical division
bl broad lamella at sclerite III in *Liphistius sensu* Kraus, 1978 (Haupt, 1983: Basalkante des Embolus)
c conductor (Menge, 1866: Spermophorum; Kraus, 1978, and Raven, 1985: sclerite III [in part])

cy cymbium (= Schiffchen, by many German authors)
da distal apophysis in the *Pisaura* genus-group
db dorsal branch of distal apophysis in *Pisaura* and *Charminus*
dtp distal tegular projection
dst distal sclerotized tube of apical division
e embolus (Menge, 1866: Eindringer; Harm, 1931, 1934: Stylus; Kraus, 1978, and Raven, 1985: sclerite III [in part])
f fundus of sperm duct
fu fulcrum
hl hyaloid lamella *sensu* Kraus, 1978, at the embolus of *Liphistius*
la lateral subterminal apophysis in *Dolomedes*
ma median apophysis (Haupt, 1983: Kontrategulum)
mh median hematodocha (Osterloh, 1922: Haematodochula)
p petiolus (Osterloh, 1922: Chitinretraktor)
pa palea in Lycosidae
pf pars fundi of the subtegulum (Loerbrocks, 1984: 386; Chamberlin, 1904: lunate plate; Osterloh, 1922: vallum chitinosum; Lamoral, 1973: ental boss of subtegulum)
pl prolateral (ental)
pp pars pendula of the embolus (Comstock, 1910: 183)
ptp proximal tegular projection in *Thaumasia* and *Tinus*
rl retrolateral (= ectal)
rta retrolateral tibial apophysis
sIII sclerite III in *Liphistius*
sa saddle (in *Dolomedes*)
ssa sail-shaped apophysis in *Pisaurina*
sd sperm duct (Osterloh, 1922: Spermakanal; Bertkau, 1875: Spermophor; Wagner, 1888: Receptaculum seminis)
st subtegulum (Wagner, 1888: s.Teg.; Osterloh, 1922: Basalschale, Patina basalis; Harm, 1931, 1934: Basalschale; Gassmann, 1925: Samenkapsel [in part]; Kraus, 1978, and Raven, 1985: sclerite I)
sta subtegular apophysis
t tegulum (Osterloh, 1922; Harm, 1931, 1934: Spermakanalkapsel; Gassmann, 1925: Samenkapsel [in part]; Kraus, 1978, and Raven, 1985: sclerite II)
ta terminal apophysis
tr truncus of the embolus (Comstock, 1910: 183; Osterloh, 1922: Chitinfaden)
vb ventral branch of distal apophysis in *Pisaura* and *Charminus*
vta ventral tibial apophysis

SYSTEMATICS OF THE FAMILY PISAURIDAE, AN UPDATE

The nursery-web, a web built by the female for the freshly hatched spiderlings, is assumed to be a characteristic feature of members of the family Pisauridae. Pisaurid females carry the spherical egg sac in their chelicerae[1] until the spiderlings are due to hatch. They then produce an irregular web and place the egg sac in its center. To date, a nursery-web has been reported from nine of the 55 pisaurid genera belonging to all three subfamilies *sensu* Simon, Pisaurinae, Dolomedinae and Thalassiinae, *see* Table I (*Afropisaura* Blandin, 1976 [*see* Blandin, 1976 and 1979b: 82]; *Dolomedes* Latreille, 1804, and *Pisaura* Simon, 1885 [*see* Gerhardt & Kästner, 1938]; *Thalassius*, Simon, 1885 [*see* Sierwald, 1989a]; *Pisaurina* Simon, 1898 [*see* Carico, 1972: 303]; *Tinus* F. O. Pickard-Cambridge, 1901 [*see* Carico, 1976: 301]; *Megadolomedes* Davies & Raven, 1980 [*see* Davies & Raven, 1980: 139]; *Architis* Simon, 1898 [*see* Nentwig, 1985: 301] and *Ancylometes* Bertkau, 1880 [*see* Merrett, 1988: 200]). So far, the nursery-web is the only synapomorphy proposed for the family Pisauridae. Thus, to assign a genus to the Pisauridae requires either the discovery of the nursery-web in such a genus or the demonstration of morphological synapomorphies relating such a genus to at least one of the nine genera listed above.

Carico (1986: 305) suggested that "a large group" of South American pisaurid genera, including the genus *Trechalea*, constitute a distinct monophyletic group, but gave no further details on the group's possible apomorphic characters. Simon described the family Trechaleidae (1890: 82; consisting of the genera *Trechalea* and *Dendrolycosa* Doleschall 1859); later he (1898: 278) listed *Trechalea* under Pisauridae. If these South American genera can be recognized as a distinct group, the family name Trechaleidae could be used (Carico's [1986: 305] statement that the name Trechaleidae is not available because it is a nomen oblitum is not corroborated by the third edition of the International Code of Zoological Nomenclature [ICZN, 1985: 260]). The spiders of this group are poorly known; all genera are currently unrevised (revisions of these genera are in preparation, *teste* Carico & Minch, 1981: 154).

The females of *Trechalea* carry the egg sac attached to the spinnerets. The egg sac is hemispherical and possesses a seam. The upper-surface is vaulted and consists of thick silk. The bottom layer is flat and the silk is thin, the eggs are visible through that bottom layer (Simon, 1898: 281; Berkum, 1982: 120). The scar of the attachment to the spinnerets is visible on the upper-surface of the egg sac even in preserved specimens. The same type of egg sac and mode of attachment was found in preserved specimens of *Hesydrus* (Venezuela; MNHN), *Dyrines striatipes* (Peru;

MHNSM), and *Syntrechalea* (Peru; MHNSM) [pers. observ.]. Apparently, *Trechalea* does not produce a nursery-web, but the spiderlings remain on the egg sac and opisthosoma of the female after hatching (Carico et al., 1985: 292, fig. 5; and pers. observ., Panama, Barro Colorado Island). It is proposed here that the structure of the egg sac represents a synapomorphy for these South American "pisaurid" genera. They all may lack a nursery-web. Unless synapomorphies can be found linking the *Trechalea* genus-group and any nursery-web pisaurid, both groups may not even be closely related[2].

The majority of the remaining pisaurid genera (circa 25) occur in Africa. Some genera (circa 5, e.g., *Perenethis* L. Koch, 1878, *Thalassius* Simon, 1885, *Euprosthenops*, Pocock, 1897) contain African and Asian species. A few genera are known from Asia and the palearctic region, with some species also in Africa (e.g., *Eurychoera* Thorell, 1897, *Pisaura* Simon, 1885, *Polybaea* Thorell, 1895, *Eucamptopus* Pocock, 1900, and *Hygropoda* Thorell, 1894). The family is represented in the Australian region (e.g., *Megadolomedes* Davies & Raven, 1980, *Inola* Davies, 1982, *Anoteropis* L. Koch, 1878). The more than 100 nominal species of *Dolomedes* Latreille, 1804, are distributed worldwide. Five genera (*see* below) of nursery-web Pisauridae (and *Dolomedes*) occur in the Americas.

Monophyletic subunits have not been defined for Pisauridae. Simon's (1898) subdivisions of Pisauridae (Pisaurinae, Dolomedinae, Thalassiinae) are still in use; Sierwald (1987) showed that his Thalassiinae is not a monophyletic clade. This study identifies one monophyletic unit within the nursery-web pisaurids, the *Pisaura* genus-group, based on apomorphies in the copulatory organs.

Thus far, the monophyly of Pisauridae is unsupported by morphological synapomorphies. The sister group is unknown. Several families have been proposed as relatives of Pisauridae: Dondale (1986: 328) used Pisauridae as a sister group to Lycosidae; Brady (1964: 436) suggested a close relationship to Oxyopidae. Lehtinen (1967) assigned the pisaurid genera to three different families, Dolomedidae (= Thaumasiinae *auct.*), Pisauridae *sensu stricto* (Pisaurinae *auct.*), and Thalassiinae in the Ctenidae. He placed Dolomedidae and Pisauridae in two different superfamilies.

Lehtinen (1967: 372) based the placement of Dolomedidae (in Lycosoidea, *see* Table 1) and of Pisauridae (in Pisauroidea; 1967: 379) on the presence or absence of a secondary conductor. Lehtinen's definitions of primary and secondary conductor (1967: 412) are ambiguous. While he defines a primary conductor "as a tegular process of variable shape and structure that acts as the primary support for the distal part of the embolus", his definition of the secondary conductor lacks details about its structure and place of attachment within the genital bulb, thus making it

impossible to identify a primary or secondary conductor. As Lehtinen's phenogram shows (page 285, fig. 6), he did not consider the conductor of *Dolomedes* and *Pisaura* as homologues but as analogous structures. The opposite position is taken in this paper as discussed later and the placement of nursery-web pisaurid genera in three families and two superfamilies is rejected.

"In cases where the primary conductor of the group concerned has lost its function, the analogous structure is called the secondary conductor (some Amaurobioidea [*sensu* Lehtinen] and Gnaphosoidea as well as all Lycosoidea), unless it is a sclerite or part of one that is generally named in another way" (Lehtinen, 1967: 412). He states (1967: 412) that "it is usually impossible to show absolute homology between different superfamilies and thus the term conductor refers to homological structures only in restricted groups." The diversity of apophyses, either reductions in certain genera or the appearance of apophyses unique to a subunit, may be great within certain families, as it will be shown in this study. Detailed data on the morphology of palpal apophyses are extremely limited and, at this point, do not allow predictions concerning homology within larger groups.

Homann (1971: 263) included Pisauridae, Ctenidae and Rhoicininae at the level of subfamilies in the Lycosidae. So far, Homann's definition of the Lycosoidea (Table 1) based on the grate-shaped tapetum of the secondary eyes, is the only suggestion for the placement of Pisauridae that is founded on a clear synapomorphy. Therefore, the palpal structures of other Lycosoidea are of special importance, since the sister group of Pisauridae is most likely to be found within Lycosoidea.

Table 1: Comparison of the classifications of Pisauridae and pisaurid subunits by Simon, Lehtinen and Levi.

Simon, 1898	Lehtinen, 1967	Levi, 1982 (based on Homann, 1971)
	Lycosoidea	**Lycosoidea**
	Cycloctenidae	
	Selenopidae	
	Lycosidae	Lycosidae
	Zoridae	Zoropsidae
Pisauridae		
Thalassiinae	Ctenidae incl. Thalassiinae,	Ctenidae
	Acanthocteninae	Acanthoctenidae
Dolomedinae	Dolomedidae (= Thaumasiinae of authors)	Pisauridae *sensu lato*, incl. Thalassiinae, Dolomedinae, Rhoicininae, Pisaurinae
	Pisauroidea	
Pisaurinae	Pisauridae (*sensu stricto*)	
	Oxyopidae	Oxyopidae
	Senoculidae	Senoculidae
	Homalonychidae	
	Toxopidae (isolated	Toxopidae
	Psechridae and derived)	Psechridae
	Amaurobioidea	
	Amaurobiidae	
	Stiphidiinae	Stiphidiidae
	Rhoicininae	
	(and Miturgidae, Amaurobiidae, Liocranidae, Agelenidae, Dictynidae, and Hahniidae)	

Forster & Wilton (1973: 15-17) listed Lycosidae, Dolomedidae and Pisauridae as having "probably been derived from Amaurobioid stock." Their Amaurobioidea include Amaurobiidae, Agelenidae, Stiphidiidae, Amphinectidae, Neolanidae, Psechridae, Ctenidae, and Cycloctenidae.

REVIEW: HOMOLOGY IN PALPAL STRUCTURES

(1) Hypotheses on the Evolution of the Male Genital Bulb

Wagner (1886, cited from Osterloh, 1922: 329) presented the following hypothesis. A cavity in the metatarsus of the pedipalp was used originally for the transfer of sperm. The metatarsus differentiated later in phylogeny to form the genital bulb. The basal hematodocha originates from the membrane of the joint between the metatarsus and tarsus; the cavity of the tarsal joint is the predecessor of the alveolus. Later (1888: 65), Wagner rejected this hypothesis and suggested that an accidental projection of the tarsus preceded the genital bulb.

Considering the structure of the intima of the sperm duct, Comstock (1910: 163) concluded that the sperm duct was an invagination of the body wall "like a trachea," surrounded by a specialized tip of the tarsus, the genital bulb.

Barrows (1925) considered the genital bulb as a homologue of the palpal claw and its teeth to be the predecessors of accessory structures (sclerites and apophyses) of the genital bulb. Harm (1931, 1934), Kraus (1978, 1984) and others followed Barrows. Kraus (1984: 374, figs. 1a-f) presented a hypothetical transformation series from a simple tarsal claw to a tripartite hydraulic bulb. Harm (1934: 133) stated that the embolus is a homologue of the tarsal claw. Raven (1985: 15) argued that the plesiomorphic state of the embolus is fully sclerotized (versus flexible and soft), since "the embolus was presumed to have been derived from the totally sclerotized tarsal claw" [*see* DISCUSSION under (**3**)].

The ontogenetic evidence (*see* below) reveals that the genital bulb is formed by the claw fundament at the distal end of the tarsus. Coddington [in press] stated that the "hypothesis that the genital bulb is a literal, transformed homologue of the palpal claw is rather decisively refuted", since rudimentary palpal claws are often contemporaneous with the developing genital bulb.

Until recently, the simple pyriform genital bulbs of Mygalomorphae and "haplogyne" spiders were considered primitive for all spiders, meaning phylogenetically old (e.g., Wagner, 1888: 65; Osterloh, 1922: 329; Gerhardt & Kästner, 1938: 530; Wiehle, 1960: 458; Barnes, 1980: 632). The more complex bulbs of entelegyne spiders were considered derived. As Gertsch (in Platnick & Gertsch, 1976) and Kraus (1978) pointed out, this hypothesis was challenged by the fact that primitive, segmented spiders (Mesothelae, Liphistiidae) possess a complex, clearly tripartite genital bulb. The Mesothelae (family Liphistiidae) are believed to be very similar to the earliest known Araneae from the Carboniferous period (300 million years ago; Foelix, 1987: 261). Today, the pyriform and simple bulbs of

Mygalomorphae and "haplogyne" spiders are regarded as secondarily simplified and therefore derived (Platnick & Gertsch, 1976; Kraus, 1978; Schult, 1983a, 1983b; Haupt, 1983; Raven, 1985; Coddington [in press]).

(2) Literature Overview

Early Studies. — The study of the structure of the male palpal organs began with the works by Blackwall (1843), Westring (1861), and Menge (1843, 1866-1879). Menge (1843: 35, pl. III figs. 13-27) distinguished three divisions and apophyses within the genital bulb. Bertkau (1875) produced the first histological sections of palps (*Segestria*) and described for the first time pores in the wall of the sperm duct. Hasselt (1889) analyzed the fine structure of the hematodocha. He found that the hematodocha does not consist of musculature as Menge believed. Wagner (1888: 65) gave schematic drawings of different palp types, and drawings of expanded genital bulbs. He used (1) the shape of the cymbium to divide the Araneae into four subgroups, and (2) the shape and the processes of the tegulum to define families.

Comstock (1910), who studied *Filistata, Hypochilus, Loxosceles, Pachygnatha, Araneus, Linyphia*, and *Dolomedes*, produced the most influential work on spider palps. His extensive nomenclature is still in use today. Since he developed the more elaborate terms for members of the Araneoidea, the use of his terms in other, unrelated groups led to serious misapplications (e.g., the median apophysis *sensu* Baum [1972, figs. 62-64] in Oecobiidae is definitely no homologue of the median apophysis *sensu* Comstock in *Dolomedes* or *Araneus* [Comstock, 1910: figs. 22, 23]). Comstock (1910: 161) was concerned about homology as his introduction showed, "we find different terms applied to homologous parts...." Obviously, he intended to apply identical terms to homologous structures. But he himself used some terms inconsistently (e.g., in *Dolomedes* [fig. 22] and *Araneus* [figs. 19, 21], the conductor clearly inserts at the tegulum, while in *Linyphia* [fig. 10], it is part of the apical division).

Osterloh's (1922) study on palps of *Linyphia, Agelena, Lycosa*, and *Meta* included histological sections as well. His drawings of the expanded palps are excellent. He assumed that the genital bulb would consist of homologous parts and tried to identify them within the species he studied. He recognized (1922: 352) the homology of subtegulum and tegulum based on morphological similarity and position within the genital bulb. He also proposed homologies of processes (= retinacula), e.g., homology of terminal apophyses in *Lycosa* and *Linyphia* (1922: 356, stema-retinaculum), but those proposals were not convincing. He described in detail the function of both male and female copulatory organs during copula.

The function of the genital bulb is still poorly understood. The modes

of sperm intake and ejaculation are not known with certainty (Harm, 1931: 645; Osterloh, 1922: 415; Wiehle, 1967: 480; Cooke, 1966; Lamoral, 1973: 638-644). Few studies have dealt with the role of particular parts of the genital bulb during copula (Heimer, 1982; Levi, 1961; Loerbrocks, 1983, 1984; Schult & Sellenschlo, 1983; Sierwald & Coddington, 1988; Gering, 1953).

Recent Studies on the Homology of Palpal Sclerites. — In numerous taxonomic monographs, the male (as well as the female) copulatory organs are well figured, but in the form of finger-print patterns for identification purposes only. Detailed morphological analyses that include discussions on homology of elements and labelling of elements are often lacking. Such drawings may furnish only limited data for future comparative and analytical studies. Several authors (e.g., Baum, 1972: figs. 49, 62-64; Gering, 1953: figs. 4, 6; Grasshoff, 1968: fig. 33; Haupt, 1983: figs. 1a-e; Heimer, 1986: fig. 1; Loerbrocks, 1984: figs. 8, 12; Merrett, 1963: figs. 1-3; Saaristo, 1971: figs. 1; Millidge, 1977: figs. 1-8; Schult, 1983a: fig. 16) produced schematic or generalized drawings of palps of the groups under study. Such drawings are especially valuable, since they present the authors concept of homology within the group studied. Additionally, such drawings illustrate more clearly the serial relationships of sclerites and apophyses. The notion that simple bulbs are primitive and complex bulbs are derived often caused the listings of plesiomorphic characters as characteristics (i.e., apomorphic) of a particular group (e.g., Millidge, 1980: 98).

Statements on homology are sometimes vague, making it difficult for subsequent workers to evaluate the presented data and conclusions (e.g., Haupt [1983: 277]: "a conductor can be found in Heptathelidae as well as in entelegynes ... [citation translated]." Judging from the context, Haupt intended to imply homology).

[In order to solve systematic problems in Linyphiidae, several attempts have been made using genitalic characters (Blauvelt, 1936; Merrett, 1963; Saaristo, 1971; Millidge, 1977; for discussion *see* Coddington [in press]). Saaristo (1971) illuminated an important autapomorphy of the linyphiid palp: the **suprategulum**, a distal prolongation of the tegular ring, which had been named median apophysis by previous authors. Saaristo showed that the suprategulum surely is not a homologue of the araneid median apophysis. All authors emphasized the problems and uncertainties of homologizing apophyses of the apical division between linyphiid genera. But especially the complex structure of the apical division (and of apophyses of the suprategulum) present the most reliable generic characters in Linyphiidae. Thus, the problems of homologizing hamper the use of these characters for phylogenetic reconstruction.]

With the general acceptance of the hypothesis that the tripartite genital bulb is plesiomorphic and that pyriform bulbs are derived, Haupt (1983, figs. 1a-e) produced a scheme in which he homologized sclerites and processes of genital bulbs in Mesothelae (*Liphistius, Heptathela*), Mygalomorphae (*Atypus, Amblyocarenum*) and Araneomorphae (*Nuctenea*, Araneidae). His proposed homologies were refuted by Raven (1985: 14-17) [*see* DISCUSSION under (**3**)].

Recently, the question of homology of palpal elements has received more attention. Griswold [in press], in his taxonomic revision of Phyxelidinae (Amaurobiidae), discussed the homology of palpal elements (and female copulatory organs) for the subfamily in detail and based taxonomic decisions on synapomorphies found in copulatory organs. Coddington [in press] presented an extensive study focusing on the homology of palpal structures, dealing with orb-weaving families (Orbiculariae) and their possible outgroups. For the first time, the homologies of median apophysis, conductor, and radix within the orb-weavers have been analyzed. He showed that these terms were often applied to structures which are not homologous even among orb-weavers but are autapomorphies for certain groups. He reviewed the available data on the ontogeny of the male spider palp and discussed their implications on homology and phylogeny for Orbiculariae. Relevant results of the ontogenetic evidence are summarized here (*see* below).

(3) Ontogenetic Evidence

The available ontogenetic evidence does not reflect the general pattern of palp ontogeny, since only very few species in disparate families have been studied (*Salticus* [Salticidae] by Wagner [1886]; *Agelena similis* [Agelenidae] by Szombathy [1915]; *Steatoda borealis* [Theridiidae], *Phidippus audax* [Salticidae], and *Lycosa nidicola* [Lycosidae] by Barrows [1925]; *Lepthyphantes nebulosa* [Linyphiidae] by Gassmann [1925]; *Segestria bavarica* [Segestriidae] and *Evarcha marcgravi* [Salticidae] by Harm [1931, 1934]; *Latrodectus curacaviensis* [Theridiidae] by Bhatnagar & Rempel [1962]; *Lycosa chaperi* [Lycosidae] by Sadana [1971]).

The claw fundament, responsible for the secretion of the dorsal claw extensor and the ventral flexor tendon, produces the male genital bulb. At a very early stage, the cell mass of the claw fundament is already divided into a dorsal and ventral lobe. The ventral lobe will form basal, middle, and apical division of the palp, including the sperm duct. The ventral lobe divides two times, first early in the development to separate the apical division from the still undivided basal and middle division of the bulb. The separation of basal and middle division (= subtegulum and tegulum) is a late event. The apophyses of the apical division develop late in

ontogeny.

The dorsal lobe of the claw fundament bifurcates very late in ontogeny (studied in *Latrodectus* only) to form two tegular apophyses (the median apophysis and the conductor in *Latrodectus*). Important in the context of this study is the status of the theridiid median apophysis. As Levi (1961: 3) already suspected, the tegular apophyses in different theridiid genera may not be homologues. Coddington [in press] concluded that those "theridiid median apophyses containing loops of the sperm duct" may just be projections or outgrowths of the tegular wall [called theridiid tegular apophysis (TTA) by Coddington]. But in certain theridiid genera (e.g., *Archaearanea, Theridion*, and *Latrodectus*), the sperm duct does not pass through the median apophysis. It is most parsimonious to assume that the tegular apophysis in *Latrodectus* is a homologue of the median apophysis as it is found in different groups of Orbiculariae (*see* Coddington [in press]) and in Pisauridae. But its homology is not established. Therefore, the ontogenetic evidence concerning the origin of the median apophysis and the conductor from the dorsal lobe of the claw fundament in *Latrodectus* allows at present no conclusions for other spider groups, not even for other Theridiidae [*see* DISCUSSION under (3)].

The ontogenetic evidence suggests that a tripartite palp is primitive and therefore subtegulum and tegulum are homologous within Araneae. The complex palpal structures in Mesothelae and in *Atypus* among the Mygalomorphae are concordant with this hypothesis.

RESULTS

(1) Morphology of Palpal Elements

The genital bulb of male spiders lies in a cavity (alveolus) of the cymbium, the modified tarsus of the pedipalp. Projections or outgrowths may occur at the patella, tibia (tibial apophyses) or cymbium (paracymbium). The genital bulb itself consists of three divisions, the basal, middle and apical (= embolic) divisions. The basal division contains a usually large, inflatable, membraneous tube, the basal hematodocha, and an often funnel-shaped sclerite, the subtegulum. Parts of the wall of the basal hematodocha may be sclerotized, forming the petiolus. The middle division consists of the median hematodocha and the sclerotized, often ring-like tegulum. The median hematodocha, connecting subtegulum and tegulum, may be large or small. The upper-surface of the tegular ring may be membraneous and sometimes inflatable. It can also be partly or totally sclerotized and more or less continuous with the tegular ring. In such cases, the tegulum appears plate-like or like an upside-down bowl.

Habitually, all structures distal to the tegulum are assigned to the

apical division (= embolic division; Osterloh [1922], Gassmann [1925]: Stema). The apical division may contain as little as the embolus alone (e.g., *Paradossenus*, Fig. 47; *Heriaeus* [Thomisidae, Loerbrocks, 1983: fig. 6]; *Evarcha* [Salticidae, Harm, 1934: figs. 1-5]; *Loxosceles* [Loxoscelidae, Comstock, 1910: fig. 4]). In certain families, it is very elaborate (e.g., in Linyphiidae and Araneidae), consisting of sclerotized tubes and membraneous tubes (often labelled distal hematodocha, Comstock, 1910: 177, figs. 13, 14; Osterloh, 1922: Stemablase), bearing the embolus and none to several processes of various size (often labelled terminal apophyses). The apical division in Pisauridae is moderately complex.

Distal Hematodocha. — The term distal hematodocha has been used for various membraneous, more or less inflatable parts within the embolic division, being either connected to the embolus or to terminal apophyses. Therefore, the term is strictly descriptive and only ambiguously defined. It is not used in the present paper.

Embolus. — The term embolus is used for that part of the genital bulb where the sperm duct opens. Comstock (1910: 182, fig. 25) described three different types of emboli, based on their shape and supposed function: the spiral embolus (occurring in many spider families, including Pisauridae), the coniform embolus (e.g., in Araneidae) and a lamelliform embolus (e.g., in Linyphiidae). He described only the spiral embolus in detail, distinguishing different structures (a sclerotized truncus and a membraneous pars pendula). Wiehle's study (1960) on different types of emboli is devoted to the function and does not give morphological details of different emboli.

At this point, it is important to note that the emboli in different families are not necessarily fully homologous [*see* DISCUSSION, (3), under Embolus].

Sperm Duct. — In most spiders, the sperm duct follows a smooth spiral from its blind end (fundus) in the subtegulum to the end of the tegulum, where it becomes very thin (ejaculatory duct). It opens at or near the tip of the embolus. More complex trajectories of sperm ducts with several switchbacks occur in a few disparate groups and are surely of non-homologous origin (and are apomorphies, whenever and wherever they are found).

Processes of the Genital Bulb

Morphological Structure. — Besides the two large, basic sclerites, subtegulum and tegulum, several sclerotized processes have been described for male palps, occurring in the middle division of the bulb as tegular processes, and in the apical division[3]. These processes have often been named apophyses, e.g., median and terminal apophyses (labelled Retinacu-

lum[4] by several German authors). The **homology of such processes** between and within different spider groups is the most ambiguous, yet crucial issue for phylogenetic reconstructions. While labelling processes many incorrect homologies have been implied.

Different **structural types of processes** can be distinguished. A process can either be formed as a distinct sclerite, separated from other sclerites by a flexible and somewhat inflatable membrane, or may be a mere projection or outgrowth of a sclerite and directly connected to it. These projections may be large and strongly sclerotized, as is the conductor in *Tinus* (Figs. 11, 13), or occur as a low hump or prominence, as the conductor in *Architis* (Fig. 42). Outgrowths of the tegulum may (or may not) contain loops of the sperm duct (e.g., in several genera of Theridiidae, Levi, 1961: figs. 5, 8, 9; labelled median apophysis). Such morphological differences, as criterion of special similarity together with the criterion of position, can be applied to recognize homologous processes. Such morphological qualities of processes are rarely considered in taxonomic monographs, descriptions and drawings.

Median Apophysis. — A median apophysis has been labelled in the palps of many spider families (e.g., Pisauridae, Araneidae, Theridiosomatidae, Oecobiidae [including Urocteidae], Lycosidae, Theridiidae, Agelenidae, Anyphaenidae, Gnaphosidae, Ctenidae, Sparassidae). The term is used almost always for a tegular apophysis. The homology of these structures is, for many groups, unstudied.

Conductor. — A conductor has always been defined by its proposed function: to protect and support the tip of the embolus (Comstock, 1910: 181; Wiehle, 1960: 460; Lamoral, 1973: 616). To my knowledge, there are no data available to support this functional assumption. It is, however, noteworthy that in many spider groups at least the tip of the embolus is in close proximity to either the tip of a tegular or an apical apophysis. Since such apophyses are usually labelled "conductor", this term has been used frequently for **surely non-homologous apophyses**, some of them inserting at the tegulum (e.g., Araneidae, Pisauridae), some of them being part of the apical division (e.g., Linyphiidae).

Terminal Apophyses. — Homologies of terminal apophyses have not been established so far. Merrett (1963) and Saaristo (1971) discussed the problems for Linyphiidae (*see* above: Literature Overview, Recent Studies). Osterloh's attempt (1922) did not yield convincing results (*see* above: Literature Overview, Early Studies).

(2) Groundplan of the Pisaurid Palpal Organ

The *Dolomedes* bulb (Fig. 2) serves as a preliminary basis of the groundplan of the pisaurid palp. It is **not necessarily thought to be**

primitive or plesiomorphic among Pisauridae. But, the *Dolomedes* palp is rich in structure and apparently not secondarily simplified. For this study, tegulum and embolic divisions are broken into discrete sectors with clear, recognizable limits and characteristic features. While analyzing bulbs of other pisaurid genera, I attempt to identify the equivalent and homologous sectors as defined in the *Dolomedes* bulb. Criteria to identify homologous elements are (a) their position within the bulb, (b) similarities

Tibial Apophysis. — The majority of Pisauridae possess an apophysis on the tibia of the male palp[5]. Usually, the tibial apophysis arises retrolaterally, at the distal end of the tibia. Its shape may be simple or very complex, but it is species-typical in all Pisauridae studied to date (e.g., Figs. 20, 21; *Thaumasia*).

Basal Division of Genital Bulb. — All Pisauridae studied possess a well-developed petiolus (Figs. 2, 13, 28; p). The petiolus is a strongly sclerotized and thickened region within the wall of the basal hematodochal membrane on the prolateral-ventral side. Its proximal tip is rounded and fits into a complementary notch in the alveolus edge (Fig. 2). Its distal tip is connected to the proximal end of the subtegulum via a tough membrane.

The subtegulum (Figs. 2, 8, 10, 11, 16, 22, 27, 31; st) is very similar in all Pisauridae studied. It forms a funnel-shaped cup. The ventral-prolateral part of the subtegulum is enlarged and often visible in the unexpanded bulb. Under this conspicuous boss (= lunate plate *sensu* Chamberlin, 1904: 174; Comstock, 1910: 176; pars fundi *sensu* Loerbrocks, 1984: 391; pf) lies the fundus (Figs. 2, 11, 37-47; f) of the sperm duct. The prolateral side of the subtegulum bears the anelli (an). The anelli are thickened sclerotized ridges. Between the anelli, the subtegular wall is split. During inflation of the bulb, the clefts are spread (Figs. 2, 13, 32). The margin of the subtegulum is a thick sclerotized rim that serves as a region of attachment for the basal and median hematodochae. The basal hematodocha is usually large. The median hematodocha is present in most genera, but sometimes only weakly developed.

Middle Division of Genital Bulb. — The tegulum (Figs. 2, 5, 14, 37-47; t) [and the apical division of the genital bulb] differs considerably among pisaurid genera and is described in detail for each genus. The tegulum is a tubular, ring-like or plate-like sclerite. The upper-surface (or distal surface) of the tegulum is membraneous and inflatable in some pisaurid genera. In other pisaurid genera, it is partly sclerotized (Fig. 37, saddle) and partly membraneous. In some Pisauridae, the distal end of the open tegular ring is enlarged to form a distinct projection (Figs. 2, 5, 16, 22, 27, 35, 49; distal tegular projection, dtp).

In many genera, the apical division is attached below the tip of the distal tegular projection by a membraneous tube. The distal end of the

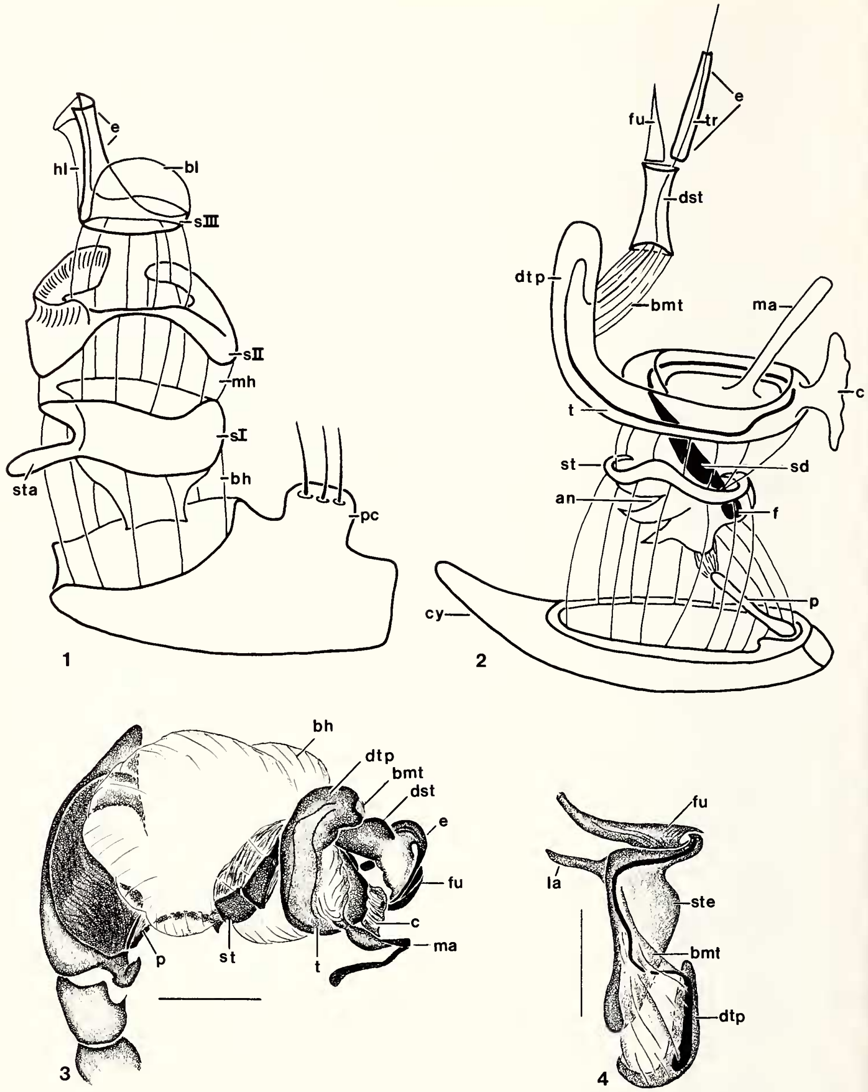


Figure 1. Schematic drawing of the male genital bulb of *Liphistius batuensis* (drawing made after descriptions and SEM-photographs by Kraus, 1978: 237, figs. 3, 4). **Figure 2.** Schematic drawing of the left expanded genital bulb of *Dolomedes.* **Figures 3, 4.** *Dolomedes tenebrosus.* **3.** Expanded left genital bulb, ventral-prolateral view. **4.** Apical division of left expanded genital bulb, retrolateral view. Scale bars: Fig. 3, 1 mm; Fig. 4, 0.5 mm.

tegulum is defined here by the distal margin of the tegular sclerite. The membraneous tube is therefore considered as the proximal part of the apical division. There are two tegular apophyses, differing both morphologically and in their relative position on the tegulum (*see* below under Tegular Apophyses).

Trajectory of Sperm Duct. — The sperm duct runs clockwise with a spiral trajectory within the subtegulum and tegulum. The fundus is located ventrally in the subtegulum, beneath the pars fundi. The sperm duct enters the dorsal part of the tegular ring (Figs. 37-47), follows the dorsal part to the retrolateral corner of the tegulum and continues its trajectory in the ventral part of the tegular ring. The sperm duct extends nearly to the tip of the distal tegular projection, turns and enters the apical division, thus forming a loop (Figs. 2, 17, 23, 30, 44). The sperm duct narrows in this region and becomes the ejaculatory duct. The loop of the sperm duct identifies the distal tegular projection.

Tegular Apophyses. — An apophysis at the retrolateral corner of the tegulum is traditionally (Comstock, Blandin, Carico) called conductor (c). The conductor inserts directly on the tegulum and appears to be a mere extension (e.g., in *Pisaura*, Figs. 7, 45) of the tegular wall. In Pisauridae, the conductor is often genus-specific, but never species-typical as the median apophysis frequently is.

Approximately halfway along the ventral part of the tegular ring, there is a second apophysis, traditionally called median apophysis (Figs. 2, 3, 5, 7-11, 16, 22, 27, 31, 34, 48, 49; ma)[6]. Positionally, the insertion of the median apophysis on the tegulum is always closer to the apical division than the insertion of the conductor. The median apophysis is attached to the tegulum via an inflatable membrane. During expansion of the genital bulb, this membrane is inflated and moves the median apophysis out of its resting position. This different mode of attachment distinguishes the median apophysis clearly from the conductor, which, as it is defined here, is immovably attached to and continuous with the tegular wall. Often, the tip of the median apophysis is distinctly sclerotized. The shape of the tip may be genus-specific (as in *Thaumasia, Pisaura*), species-group-specific (as in the *tenebrosus*- and *fimbriatus*-groups of *Dolomedes*; Carico, 1973: figs. 25-33) or species-typical (as in *Thalassius*; Sierwald, 1987: figs. 1, 2, 54, 55, 58-68, 126, 127).

The terms median apophysis and conductor, as defined here, denote homologous structures in all pisaurid genera.

Apical Division. — The apical division consists of a basal membraneous tube (bmt) and a distal sclerotized tube (dst). The ejaculatory duct extends through the basal membraneous and the distal sclerotized tubes. Proximally, the basal membraneous tube is connected directly to the distal

tegular projection. Distally, it is connected to the sclerotized tube. The distal end of the sclerotized tube bears the embolus. None to several apophyses may be attached to both the basal membraneous [e.g., the distal apophysis (da) in *Pisaura*; Fig. 7] and distal sclerotized tubes [e.g., the fulcrum (fu) in *Dolomedes*; Fig. 6].

Embolus. — In most Pisauridae studied to date, the embolus can be described as the spiral type *sensu* Comstock (1910: 181, 183). It consists of a strongly sclerotized, gutter-like sclerite on its convex side (truncus of the embolus, tr; Figs. 2, 14, 15). The truncus is basally broad and scoop-shaped. It narrows distally. The concave side is covered by a membrane (pars pendula, pp; Figs. 15, 17, 27, 30), thus forming a tube. The pars pendula is large and inflatable in certain genera (members of the *Pisaura* genus-group).

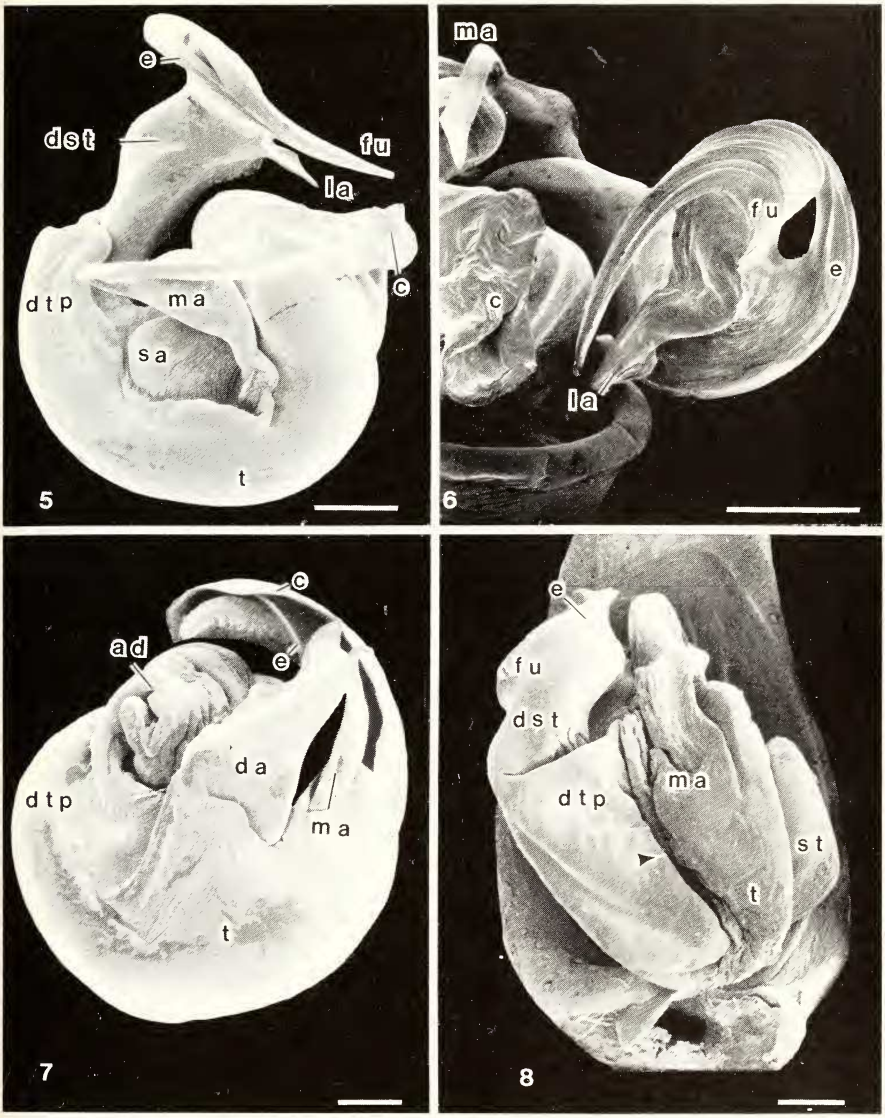
(3) Palp Morphology in American Nursery-Web Pisauridae

Carico (1973, 1972, 1976, 1981) provided good illustrations of the male copulatory organs in the American species of *Dolomedes, Pisaurina, Tinus, Architis*, and *Staberius*. The results obtained through the present study suggest new and different interpretations of certain parts of the organs. The genus *Thaumasia*, distributed in Central and South America, is unrevised (revision in preparation, Carico, pers. communic.). Therefore, the use of *Thaumasia* species-names has to be regarded as provisional. Their copulatory organs are still poorly known.

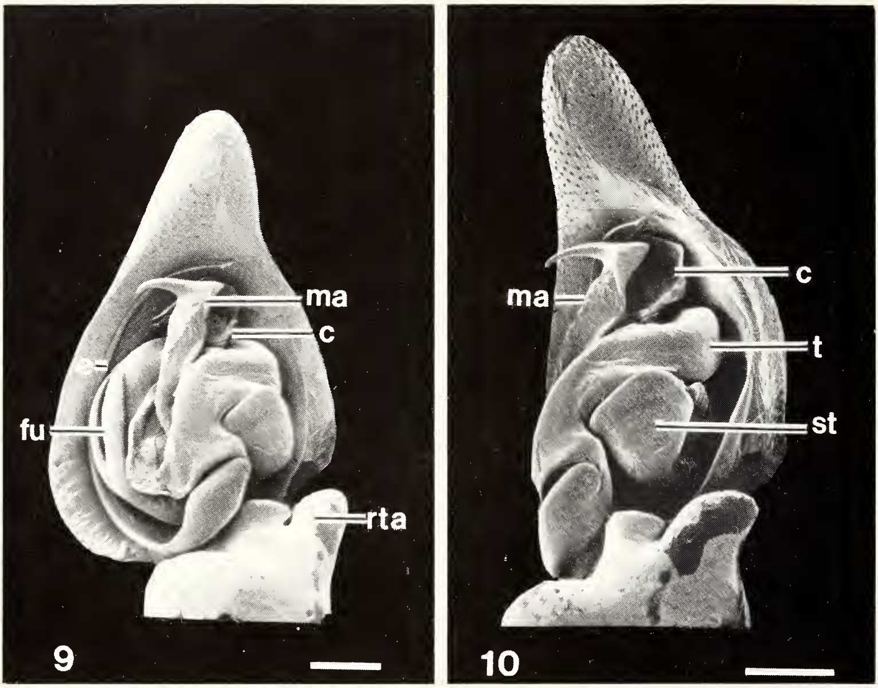
Dolomedes Latreille, 1804 (Figs. 2-6, 37)

The tibial apophysis is large. The median hematodocha is present. The tegulum is an open spiral (Fig. 37), not a closed ring, with a single loop. The distal end of the tegular ring somewhat overlaps the proximal end and forms a distinct distal tegular projection. The outer margins of the tegular ring are rounded and U-shaped in cross section with the closed portion being peripherally located. The upper-surface of the tegular ring is partly sclerotized forming a saddle (Fig. 37, sa). The conductor is thin, membraneous and lamelliform (Figs. 3, 5). The tip of the median apophysis is sclerotized and flat. The apical division of the bulb (Figs. 3-6) contains the basal membraneous tube (bmt) and the distal sclerotized tube (dst). In the *tenebrosus*-group, the latter is very large and clearly visible in the unexpanded palp (Fig. 5); it is somewhat smaller in the *fimbriatus*-group.

The distal end of the sclerotized tube (Figs. 4-6) bears a sclerotized lamelliform apophysis (= lateral subterminal apophysis, Comstock, 1910: 181; lsta). Juxtaposed to this apophysis, another terminal apophysis called fulcrum (Comstock, 1910: 181; fu) and the embolus arise (Figs. 4-6). In



Figures 5-8. SEM-photographs, unexpanded left genital bulb. **5.** *Dolomedes tenebrosus*. **6.** *Dolomedes tenebrosus*, apical division. **7.** *Pisaura mirabilis*. **8.** *Thalassius rubromaculatus*. Scale bars: 0.25 mm.



Figures 9, 10. *Thalassius spinosissimus,* unexpanded left genital palp. **9.** ventral view. **10.** retrolateral view. Scale bars: 0.25 mm.

the *tenebrosus*-group, the distal margin of the fulcrum is tightly wrapped around the embolus. In the *fimbriatus*-group, the embolus follows a furrow of the convex side of the fulcrum.

In *Dolomedes,* the embolus appears to consist of the truncus alone, the pars pendula is not well developed.

Tinus F. O. Pickard-Cambridge, 1901 (Figs. 11-15, 38)

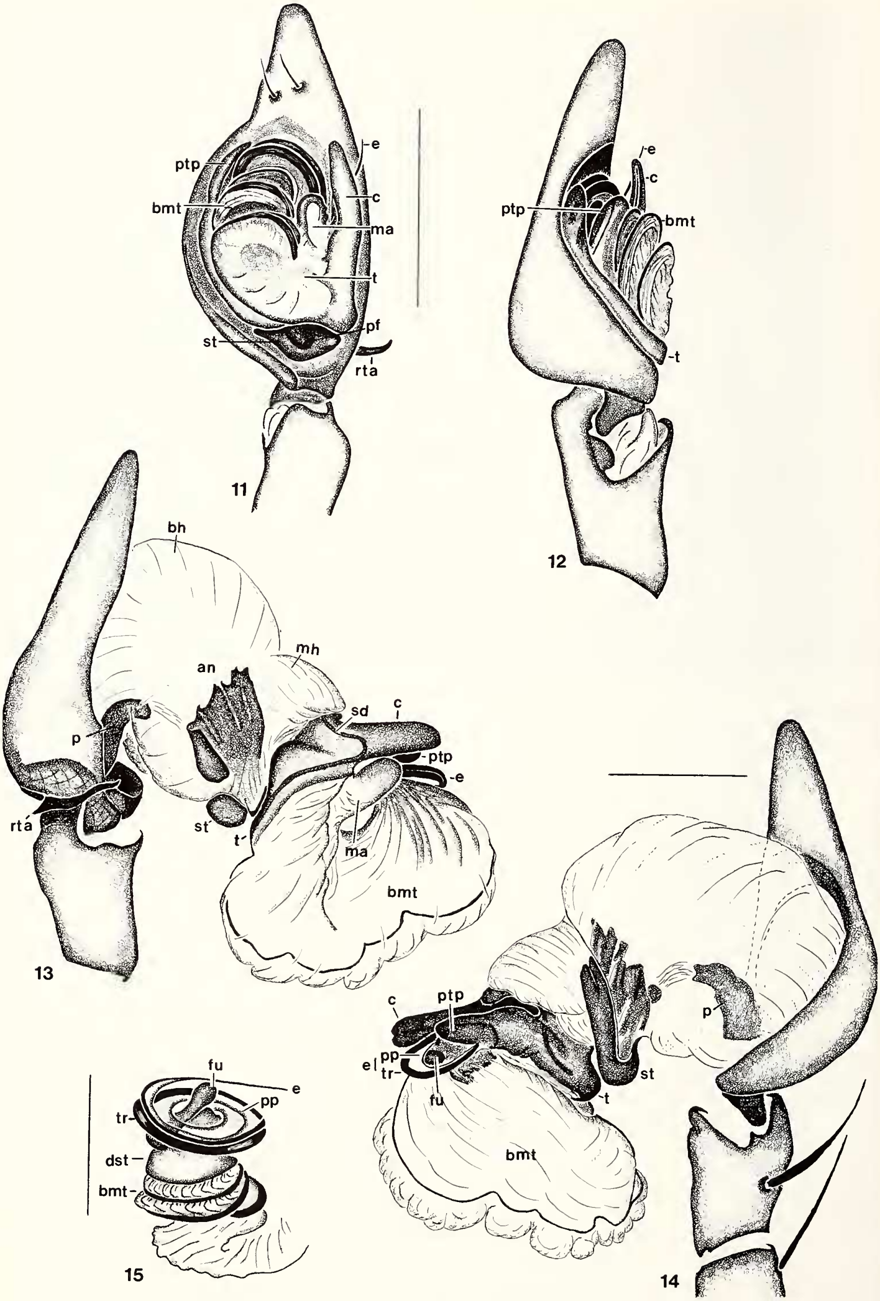
The conspicuous tibial apophysis in *Tinus* arises in a more dorsal position and bends retrolaterally. The median hematodocha is well developed. The tegulum bears three processes (Fig. 11). Following the sperm duct from the fundus in the subtegulum into the dorsal portion of the tegulum, one encounters a large process of the tegulum on the prolateral side of the bulb (proximal tegular projection, ptp; Figs. 11, 12, 14, 38). This process is stiff and sclerotized. Next to the large conductor on the retrolateral side is the median apophysis in the ventral sector of the tegular ring. The median apophysis is rather short, flat, rounded at the tip and shaped like a spatula. Only its tip is slightly sclerotized.

After passing the median apophysis, the sperm duct enters a large membraneous sac (= tegulum *sensu* Carico, 1976: figs. 6, 7). The sperm duct is very slender in this section, thus forming the ejaculatory duct. It follows the outer margin of the sac. In the unexpanded bulb, this sac is coiled. The number of loops is species-typical (Fig. 15; Carico, 1976: figs. 8-17). In the left, unexpanded palp (ventral view), the tegular sac is twisted ascending-counterclockwise (Fig. 38). Distally, the sac is closed by a small, strongly sclerotized tubercle (Fig. 15). Additionally, the tip bears a sclerotized rounded projection. The long embolus arises here. Its proximal part shows clearly that it consists of a peripheral sclerite on the convex side, the truncus, and a membraneous part on the concave side, the pars pendula. The remaining part of the embolus is long, whip-like and forms three loops. It is coiled ascending-clockwise (left unexpanded palp in ventral view; Figs. 15, 38).

Thaumasia Perty, 1833 (Figs. 16-21, 41)

In the genus *Thaumasia*, the tibial apophyses of different species are large and complex. They appear to be species-typical (Fig. 20: *Thaumasia* cf. *uncata*, and Fig. 21: *Th.* cf. *velox*). A median hematodocha was not observed during inflation of the bulb. [This may be due to incomplete inflation, since old preserved material was used. The basal hematodocha also did not expand well.]

The tegulum (Fig. 41) is rather similar in structure and position to the one in *Tinus*. Immediately upon the entry of the sperm duct into the tegulum on the prolateral side, the tegular wall bears a low broad hump (Fig. 41). This hump is not visible in the unexpanded bulb, since it lies behind the large distal tegular projection. In *Thaumasia* cf. *velox* this hump is scoop-shaped and its form is similar to the proximal tegular apophysis (ptp) in *Tinus* in the same position, hence considered homologous. The tegulum bears three conspicuous processes that are visible in the unexpanded bulb (Figs. 16, 17). At the retrolateral side, there is a long, slender apophysis that is slightly sclerotized. Its tip is swollen, sclerotized, and tilted. Because of its position and its type of connection to the tegular ring, it is considered to be the conductor. The conductors in *Tinus* and *Thaumasia* are similarly large, but in *Tinus* strongly sclerotized and of different shape. The median apophysis is short, broad, flat and similar to the one found in *Tinus*. In *Thaumasia* however, it is bifurcated (in cf. *uncata* and cf. *velox*). The third process on the retrolateral side of the bulb is long, shaped like a duckbill and sclerotized. The sperm duct extends to its tip and undergoes a large loop within it. On its dorsal side, the sperm duct narrows and runs down to enter the embolic division.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From its position and the trajectory of the sperm duct this process is clearly the distal tegular process, homologous to that found in *Dolomedes*.

The apical division consists mainly of the embolus. The embolus arises at the basal part of the distal tegular projection and branches off it in a nearly right angle. The embolus is connected to the distal tegular projection by a membrane. Within this membrane lie two small sclerites (Fig. 18; sc). Both are connected to the basal section of the embolus, the retrolateral sclerite is attached via a membraneous bridge, and the prolateral sclerite is directly attached to the base of the embolus. The proximal section of the embolus (Figs. 16, 17) shows clearly the truncus at the convex side and the pars pendula at the concave side. The base of the truncus is enlarged; its base fits into a notch in the proximal tegular projection (ptp).

Architis Simon, 1898, and ***Staberius*** Simon, 1898 (Figs. 22-26, 39, 42)

The morphology of the genital bulbs in both genera is very similar. Whereas *Architis* currently contains seven species, *Staberius* is monotypic (Carico, 1981). Therefore, synapomorphies for *Architis* (excluding *Staberius*) cannot be defined at this point. Characters listed here for *Staberius* may be autapomorphies for a single species and do not justify a separate genus.

In *Architis*, the tibial apophyses are complex and species-typical. In *Staberius spinipes*, the tibia bears a large hammer-shaped ventral apophysis in addition to the retrolateral apophysis (*see* Carico, 1981: figs. 34, 35). The ventral tibial apophysis is connected to the tibia via a flexible membrane. The retrolateral apophysis in *Staberius* is a conspicuous process pointing laterally.

In the unexpanded bulb (Fig. 22; Carico, 1981: figs. 12-23, 34) the tegulum and its distal projection are the prominent structures. The tegular ring is rather small; its distal projection is large. There are two small apophyses on the tegulum, barely visible in the unexpanded bulb (Figs. 22, 39, 42). The conductor, juxtaposed to the distal tegular projection, is a small hump-shaped tubercle. The median apophysis is short and membraneous. Only its tip is slightly sclerotized. The sperm duct does not progress straight through the tegular ring, but performs two curves. The sperm duct extends to the tip of the distal tegular projection and performs a loop. At that point, it starts to narrow becoming the ejaculatory duct (Figs. 25, 26). The ejaculatory duct enters a large, less sclerotized hump that is mesally attached to the distal tegular projection. The

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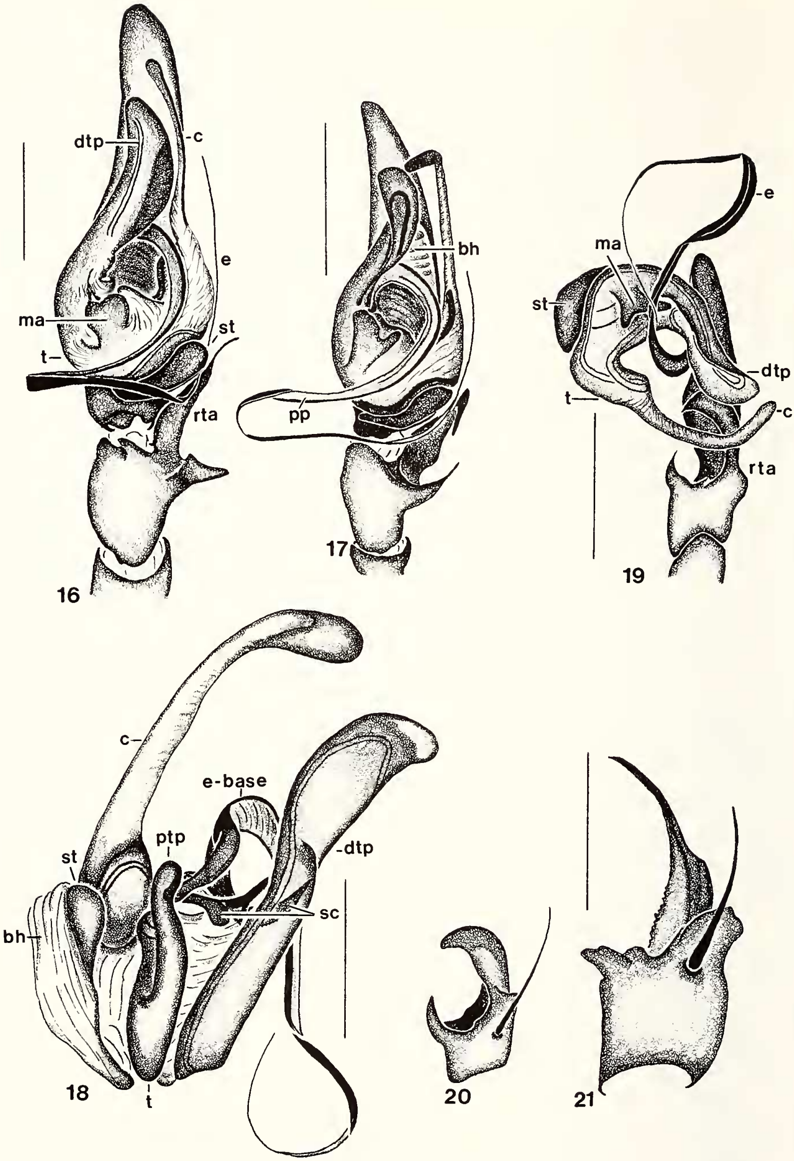
Figures 11-15. Left palp of *Tinus peregrinus*. **11.** Unexpanded bulb, ventral view. **12.** Unexpanded bulb, prolateral view. **13.** Expanded bulb, retrolateral view. **14.** Expanded bulb, prolateral view. **15.** Apical division. Scale bars: Figs. 11-14, 1 mm; Fig. 15, 0.5 mm.



Figures 16-21. Left palp of *Thaumasia*. **16.** *T.* cf. *velox*, unexpanded, ventral view. **17.** *T.* cf. *uncata*, unexpanded, ventral view. **18.** *T.* cf. *uncata*, genital bulb, partly expanded, prolateral view, sc = sclerites. **19.** *T.* cf. *uncata*, expanded, retrolateral view. **Figures 20, 21.** Tibial apophyses. **20.** *T.* cf. *uncata*. **21.** *T.* cf. *velox*. Scale bars: Figs. 16, 17, 19-21, 1 mm; Fig. 18, 0.5 mm.

sclerotized embolus branches off dorsally from this hump (Figs. 39, 42). The base of the embolus is broad, consisting of the truncus and pars pendula.

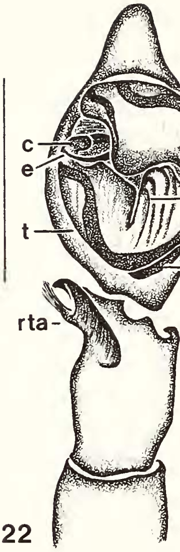
Pisaurina Simon, 1898 (Figs. 27-29, 44)

In this genus, the tibial apophysis is small. At the distal tip of the tibia in *Pisaurina mira*, there is a broad, flat, sclerotized structure. It can be considered a ventral tibial apophysis (Fig. 27, vta). The petiolus is very broad (Fig. 28). The tegulum is plate-like (Fig. 44) and lies flat in the alveolus, thus its position is very different from all other American Pisauridae. The tubular outer rim of the tegulum containing the sperm duct is strongly sclerotized, the upper-surface is sclerotized to a lesser degree, but not membraneous. On its retrolateral side the tegulum produces a hump with a spur (Figs. 27, 44; dtp). The sperm duct extends to the distal tip of this hump and performs a loop turning back.

The apical division of *Pisaurina* consists of three sclerotized bulbous sections (ad I, II, III). The prolateral side of these three sections is membraneous; the membrane visible at the proximal end of the genital bulb (Fig. 27, bmt) is part of it. At the distal end of the second bulbous section the sperm duct narrows to become the ejaculatory duct. Attached to the distal region of the third bulbous section is a membrane, regarded here as the pars pendula of the embolus. The pars pendula is clearly separated by a sclerotized section from the bmt-membrane. The embolus is extremely long, thin and whip-like. Over much of its course, it appears to consist of the ejaculatory duct alone. The broader, basal part of the truncus appears to be fused to the third bulbous section of the apical division.

There are two conspicuous apophyses, one of which can be identified as the median apophysis. The latter possesses a bifurcated sclerotized tip (similar to *Thaumasia*) and a membraneous base. It is attached to the membraneous central area of the plate-like tegulum. Its tip rests in the spur of the distal tegular hump.

The second apophysis, labelled here sail-shaped apophysis (ssa; labelled conductor by Carico, 1972), is large, flat and sail-shaped, ending in a long spur. Its base is membraneous, with a sclerotized strap attached to the second bulbous section of the apical division. Its outer margin is sclerotized and lamellar. It is wrapped around the thin embolus. In the undisturbed bulb, the embolus extends to the tip of the sail-shaped apophysis. Apparently, this feature caused its misidentification as a conductor. But neither its position nor its mode of attachment to the tegulum and to the second bulbous section of the apical divisions warrants this homology-



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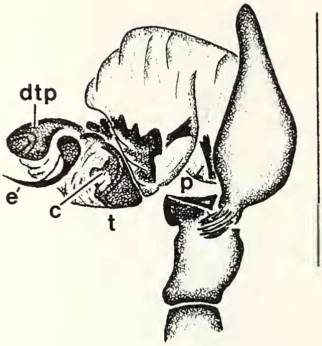

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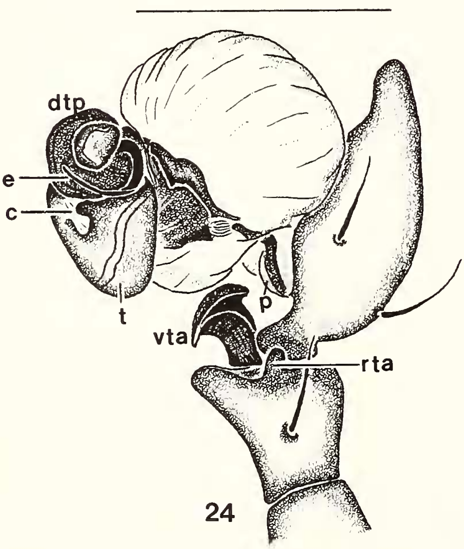

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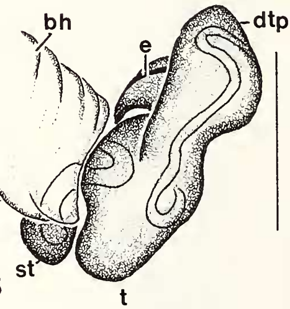

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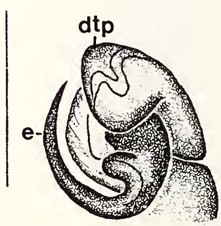

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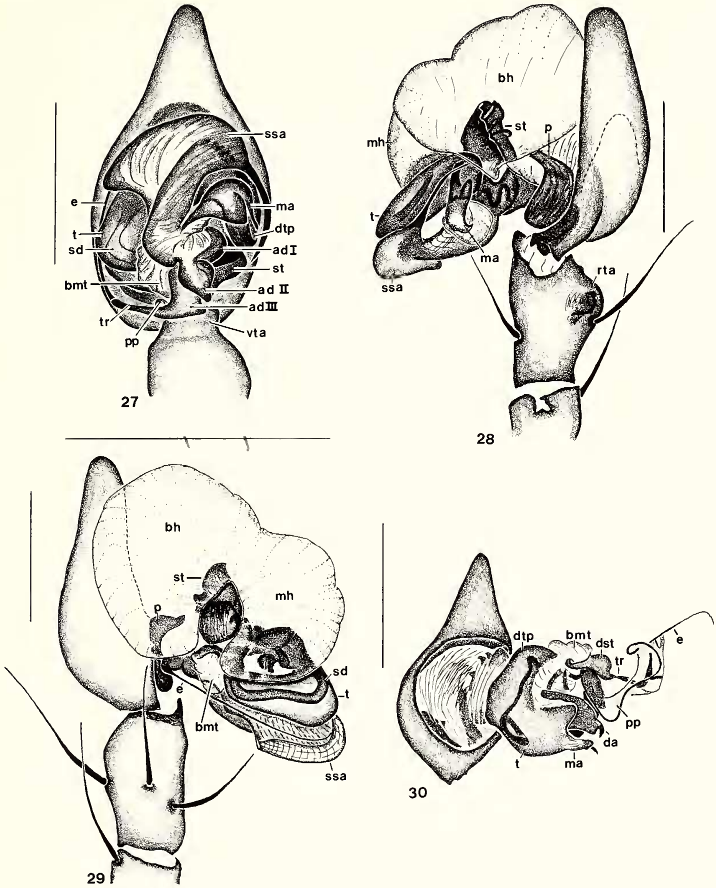
Figures 22, 23. *Architis tenuis.* **22.** Unexpanded right bulb, ventral view. **23.** Expanded left palp. **Figures 24-26.** *Staberius spinipes.* **24.** Expanded left palp, retrolateral view. **25.** Tegulum, prolateral view. **26.** Distal tegular projection and apical division, retrolateral-dorsal view. Scale bars: Figs. 22, 25, 26, 0.5 mm; Figs. 23, 24, 1 mm.



Figures 27-29. *Pisaurina mira,* left palp. **27.** Unexpanded, ventral view. **28.** Expanded, retrolateral view. **29.** Expanded, prolateral view. **Figure 30.** *Pisaura mirabilis,* left expanded palp, ventral view. Scale bars: 1 mm.

hypothesis. The tip of the sail-shaped apophysis lies parallel to the upper branch of the tip of the median apophysis.

(4) Palp Morphology in Other Nursery-Web Pisauridae

Pisaura Simon, 1885 (Figs. 7, 30, 45)

The tibial apophysis is thick and tubular, bearing brushes of hair in some species. The upper-surface of the tegulum is mostly sclerotized, thus the tegulum is bowl-like, with the sperm duct following the outer margins of the bowl. The upper-surface of the tegulum surrounding the distal

tegular projection is membraneous, strongly inflatable, and continues to become the basal membraneous tube (Fig. 30). The most prominent features of the *Pisaura* bulb are **three** conspicuous apophyses (Fig. 7; c, ma, da). The conductor at the retrolateral side of the genital bulb is large and sclerotized. The next apophysis is smaller, with a hook-shaped tip. Because of its position and membraneous attachment to the tegulum, it is considered to be the median apophysis.

The distal apophysis, situated distad of the median apophysis (Figs. 7, 45) is large, consisting of a dorsal branch and a ventral branch (Fig. 45, db, vb). The dorsal and ventral branch are fused distally and form a distinct hook. The ventral branch anchors the distal apophysis in the tegulum with a membraneous connection. The dorsal branch is attached to the membraneous upper-surface of the tegulum and extends towards the distal sclerotized tube of the apical division. From the ventral branch a sclerotized clasp, also attached to the membraneous upper-surface of the tegulum around the distal tegular projection, extends to the basal membraneous tube of the apical division. Therefore, the distal apophysis is connected to both the middle and apical division of the genital bulb.

The apical division (Fig. 30) consists of a rather large basal membraneous tube, the distal, sclerotized tube and a spiral embolus with a large, flag-like pars pendula. The truncus of the embolus is fused to the distal end of the sclerotized tube. Within the wall of the pars pendula lies a thin, T-shaped sclerite.

Blandin (1976) described the genus *Afropisaura* for African species formerly assigned to *Pisaura*. He based his decision on differences in features of male and female copulatory organs (Blandin, 1976: 928, figs. 17, 18). The species remaining in *Pisaura* comprise four to six species besides *mirabilis*, occurring in the palearctic region (*see* Brignoli, 1984). The genus *Pisaura* is in need of revision.

Approximately 20, mainly African genera possess the same basic bulb configuration as *Pisaura* (Fig. 45): a bowl-like tegulum, a large conductor, a slender median apophysis with a pointed, curved tip, and a large distal apophysis comprised of two branches. In certain genera, such as *Charminus* Thorell, 1899 (Figs. 49-51), the conductor is morphologically more complex. It consists of a sclerotized convex retrolateral part. This sclerotized part is connected directly to the tegular ring. The inner, concave side is an inflatable membrane, and actually a continuation of the upper-surface of the tegulum. During inflation, this inner part of the conductor, and also the basal membraneous sections of the median apophysis are expanded.

The apical divisions of the genera of the *Pisaura* genus-group show a wide range of diversity and are genus-specific.

Thalassius Simon, 1885 (Figs. 8-10, 40, 43)

The tibial apophysis is reduced (*see* Sierwald, 1987). The tegulum (Figs. 40, 43) forms a tubular ring with a membraneous center. The conductor is membraneous and very similar to the one found in *Dolomedes*. The median apophysis is large; its tip is heavily sclerotized and species-typical (Sierwald, 1987, figs. 54-55, 58-61, 126, 127).

In the *rubromaculatus*-group, the distal tegular projection is large; it possesses a somewhat less sclerotized zone (Fig. 8, arrowhead; Fig. 40, meandering line). The apical division consists of a single, solid sclerite, whose shape is very similar to the distal sclerotized tube and fulcrum combined as it occurs in *Dolomedes tenebrosus* (Fig. 3). The apical division is connected to the distal tegular projection via a short basal membraneous tube.

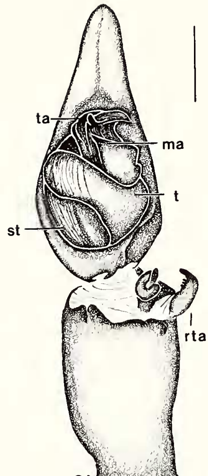
In the *spinosissimus*-group, the distal tegular projection appears to be reduced. The apical division consists of a basal bulbous section, a conspicuous, sclerotized finger-shaped apophysis (Fig. 43, fu), and a long, whip-like embolus. The finger-shaped apophysis is attached to the sclerotized bulbous section via a membrane and is considered here a homologue of the fulcrum.

(5) Palp Morphology in the South American *Trechalea* genus-group

For many of the genera in this group, the copulatory organs have never been figured in sufficient detail. For the present study, the palps of *Trechalea* (22 nominal species) and *Paradossenus* (three nominal species) are analyzed. Additionally, I conducted preliminary studies on palps of *Dyrines striatipes, Enna* sp., *Hesydrus* sp. and *Syntrechalea porschi*. The results reveal features justifying the separation of these spiders from the remaining nursery-web Pisauridae.

Trechalea Thorell, 1870 (Figs. 31-33, 46)

The tibial apophysis consists of two branches (Fig. 31; Carico & Minch, 1981, figs. 1, 2). The body wall between both branches is membraneous. The tegulum forms a ring. The ventral section of the tegular ring is broad; the sperm duct performs seven loops within this section of the tegulum. The conductor is a broad, low hump and only visible in the expanded palp. The median apophysis is a massive structure with two stout branches. Its shape and structure is considerably different from the median apophyses occurring in nursery-web Pisauridae, thus representing another character state. The apical division consists of a short thin embolus and a large terminal apophysis, bearing three small finger-shaped projections.



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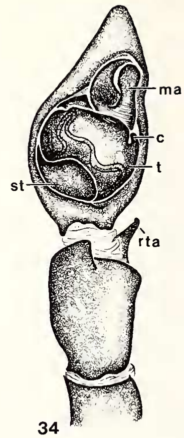

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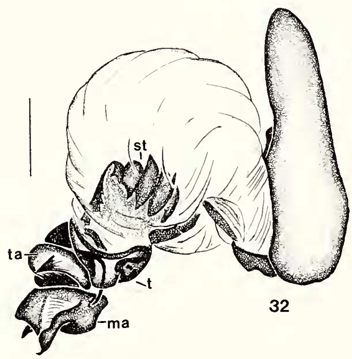

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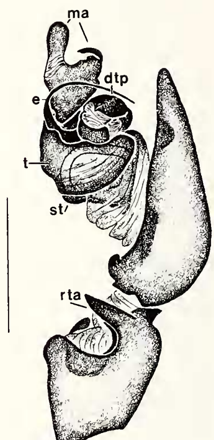

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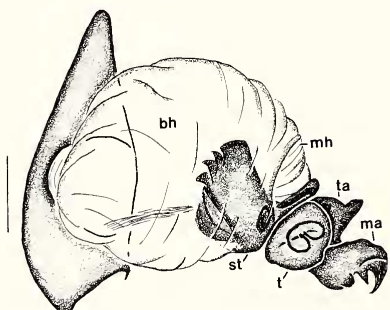

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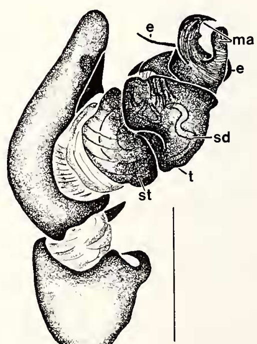

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Paradossenus F. O. Pickard-Cambridge, 1903 (Figs. 34-36, 47)

The tibial apophysis consists of a spur pointing ventrally. The body wall beneath it forms a deep membraneous pit. The tibial apophysis of *P. taczanowskii* Caporiacco, 1948, agrees with the figure given by F. O. Pickard-Cambridge (1903: figs. 7-9) in the original description of *P. nigricans*. These species are here regarded to be synonymous. The tegulum is ring-like, the ventral section is well developed as in *Trechalea*. The sperm duct performs five loops in the ventral section of the tegulum. The conductor is a small, inconspicuous projection of the tegular wall. As in *Trechalea*, the median apophysis forms a massive cubic structure with two stout branches. The distal tegular projection is well developed (Fig. 35). The apical division consists of a short basal membraneous tube and a slender sclerotized tube, which is fused to the embolus. There are no terminal apophyses (Fig. 47).

The palps of *Dyrines*, *Enna*, *Hesydrus* and *Syntrechalea* possess several identical characters with *Trechalea* and *Paradossenus*: a small, reduced conductor, the massive median apophysis with two branches, a coiled sperm duct with several switchbacks (except perhaps *Dyrines*), and a conspicuous membraneous pit at the distal end of the tibia.

DISCUSSION

(1) Homology of Palpal Elements Within Pisauridae and Evaluation of Character States

Tibial Apophysis. — The *Trechalea* genus-group possesses a synapomorphic character in the form of a membraneous pit that accompanies the tibial apophysis. A membraneous pit is also present in *Rhoicinus* Simon, 1898 (*see* Exline, 1960: fig. 2), whose relationship is uncertain, but has been placed in the Pisauridae by various authors.

Distal Tegular Projection. — The distal tegular projection can be identified by the loop of the sperm duct within it, its distal position and the attachment site of the apical division being below the tip of the projection. It occurs clearly in *Dolomedes*, *Pisaura*, *Architis/Staberius*, *Thaumasia*, the *Thalassius rubromaculatus*-group, and *Paradossenus*. In *Pisaurina*, the retrolaterally situated hump with the spur is considered here

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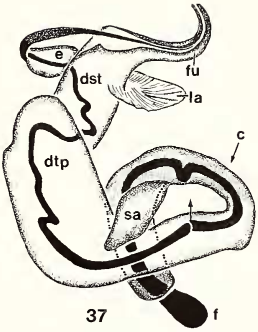
Figures 31-33. *Trechalea* sp., left palp. **31.** Unexpanded, ventral view. **32.** Expanded, retrolateral view. **33.** Expanded, prolateral view. **Figures 34-36.** *Paradossenus nigricans*, left palp. **34.** Unexpanded, ventral view. **35.** Expanded, retrolateral view. **36.** Expanded, prolateral view. Scale bars: 1 mm.



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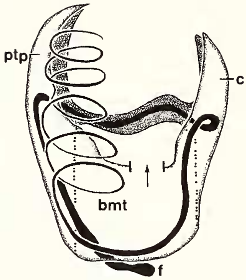

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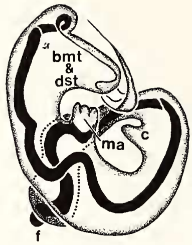

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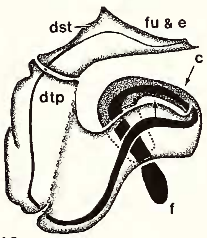

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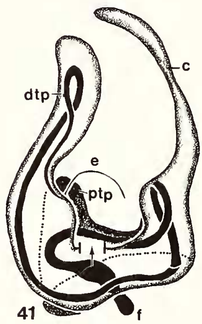

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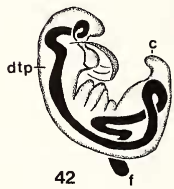

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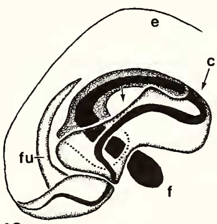

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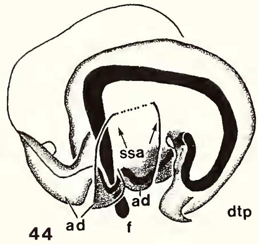

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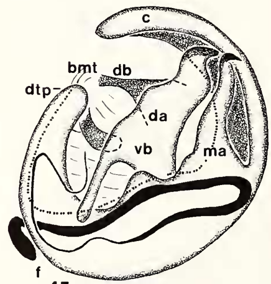

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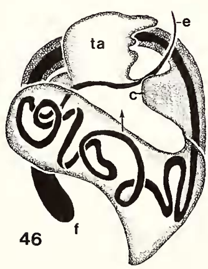

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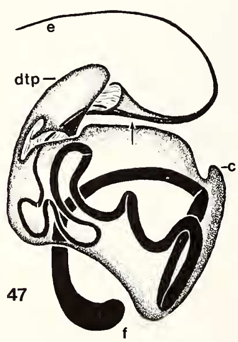

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to be homologous with the distal tegular projection of the other genera because it contains the loop of the sperm duct and because its position relative to the attachment of the apical division. The genital bulbs of *Tinus* and the *Thalassius spinosissimus* species-group probably lost this feature secondarily and independently. The distal tegular projection is absent in the *Trechalea* genus-group.

Median Apophysis. — All genera studied here possess a median apophysis. The median apophysis occurs in a variety of different character states, its general structure being always autapomorphic at the generic level. Additionally, it can be species-typical (*Thalassius*), or species-group specific (*Dolomedes*). The character state of the median apophysis in *Architis/Staberius* is considered a reduction, therefore derived. In the *Trechalea* genus-group, the morphology of the median apophysis differs distinctly from the median apophysis of the nursery-web Pisauridae, thus this character state is a synapomorphy for the South American *Trechalea* genus-group.

Conductor. — The conductor occurs in several morphological conditions (character states): it is membraneous in *Dolomedes* and *Thalassius* (synapomorphy); it is long in *Thaumasia*, and large, stiff, and heavily sclerotized in *Tinus*. In the *Pisaura* genus-group it is large as well, but in several genera the concave side of the conductor consists of an inflatable membrane of variable size, which is a continuation of the upper-surface of the tegulum. The conductor is small in *Architis/Staberius* and the *Trechalea* genus-group, and absent in *Pisaurina*. These reductions are independently derived.

Apical Division. — The apical division of the genital bulb shows a wide range of diversity: its appearance is usually genus-specific. The basal membraneous tube occurs in all pisaurid genera studied so far: the sclerites of the apical division were always found to be connected to the distal tegular process via an inflatable membrane. The basal membraneous tube

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Figures 37-47. Schematic drawings of tegula, trajectory of sperm duct black, arrows indicate insertion of conductor (c), sail-shaped apophysis (ssa) and median apophysis (unmarked arrow). **37.** *Dolomedes tenebrosus*, conductor and median apophysis omitted. **38.** *Tinus peregrinus*, median apophysis omitted, embolus cut off. **39.** *Staberius spinipes*. **40.** *Thalassius rubromaculatus*, conductor and median apophysis omitted. **41.** *Thaumasia* cf. *uncata*, median apophysis omitted, embolus cut short. **42.** *Architis tenuis*. **43.** *Thalassius spinosissimus*, conductor and median apophysis omitted. **44.** *Pisaurina mira*, median apophysis and sail-shaped apophysis omitted. **45.** *Pisaura mirabilis*, tegulum including conductor, median apophysis and distal apophysis. **46.** *Trechalea* sp., median apophysis omitted. **47.** *Paradossenus nigricans*, median apophysis omitted.

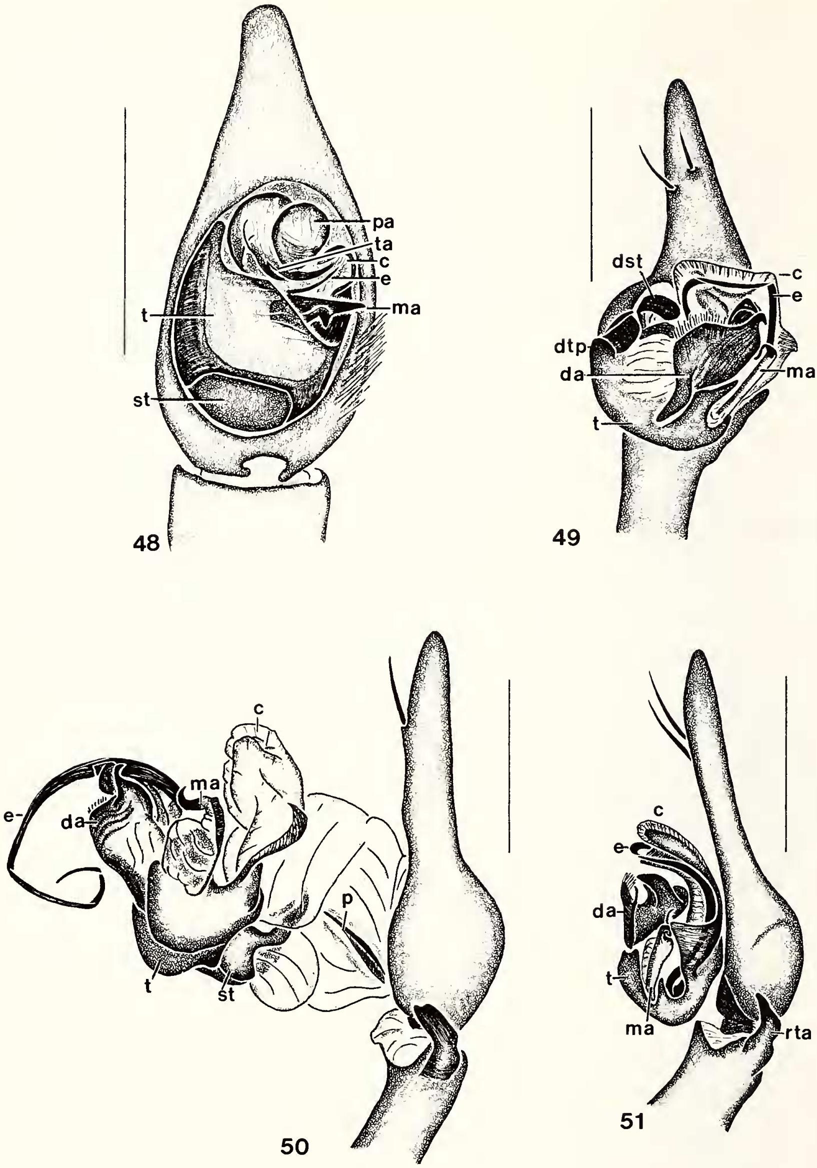

Figure 48. *Trochosa ruricola,* left unexpanded palp, ventral view. **Figures 49-51.** *Charminus camerunensis.* **49.** Left unexpanded palp, ventral view. **50.** Expanded left palp, retrolateral view. **51.** Unexpanded left palp, retrolateral view. Scale bars: 1 mm.

varies in size. It is very small in *Thalassius*. The membraneous sac in *Tinus* is interpreted as a complexly developed basal membraneous tube of the apical division, based on the fact that the sperm duct forms the ejaculatory duct within it.

The distal sclerotized tube is clearly present in *Dolomedes*, *Tinus*, and the *Pisaura* genus-group; the *Thalassius rubromaculatus*-group possesses a homologue that is fused to the distal tegular projection and to the fulcrum. The presence of the distal sclerotized tube is considered the plesiomorphic condition. In *Pisaurina*, it may be represented by the second bulbous section of its apical division (*see* below). In *Thaumasia*, several small sclerites are present at the base of the embolus; they may represent homologues of the sclerotized tube and/or terminal apophysis. In *Architis* and *Staberius*, the basal membraneous tube and the distal sclerotized tube appear to be fused to the broad hump that is attached to the distal tegular projection. In *Paradossenus*, the distal sclerotized tube is reduced in size and fused to the base of the embolus. The distal sclerotized tube is absent in *Trechalea*.

Apophyses of the Apical Division. — The genera in question show a variety of terminal apophyses. The fulcrum is defined as an apophysis attached to the distal end of the distal sclerotized tube. The fulcrum in both *Thalassius* species-groups is considered homologous to the *Dolomedes* fulcrum because of its position and similarity in shape. The club-shaped terminal apophysis in *Tinus* (Fig. 15) is considered here to represent a homologue of the fulcrum as well. The subterminal lateral apophysis in *Dolomedes* is an autapomorphic feature of this genus.

Distal Apophysis and Sail-Shaped Apophysis. — The distal apophysis in the *Pisaura* genus-group may be homologous to the sail-shaped apophysis in *Pisaurina*. Both are attached to the tegulum in the membraneous area surrounding the distal tegular projection. Their position and connections to the middle and apical divisions support this hypothesis. Since the sail-shaped apophysis in *Pisaurina* is connected (via the sclerotized strap) to the second bulbous section of the apical division, the second bulbous section could be considered a homologue of the distal sclerotized tube. This homology-hypothesis is speculative. It could be supported or refuted by the presence or absence of further concordant homologies in the female copulatory organs or somatic characters. *Pisaurina* displays a sexual behavior (using silk to wrap the female's legs [Bruce & Carico, 1988[7]]) that is different from the copulatory behavior in *Pisaura mirabilis*.

Blandin (1976: 923, figs. 8, 9, 13, 14) labelled the distal apophysis in *Pisaura* as the fulcrum. Since the term fulcrum is used for an apophysis attached to the distal end of the sclerotized tube of the apical division, the fulcrum *sensu* Comstock is not homologous to the distal apophysis in

Pisaura.

Trajectory of Sperm Duct. — In most genera studied, the sperm duct forms a simple loop, which presumably represents the plesiomorphic condition. The *Trechalea* genus-group is characterized by several switchbacks of the duct in the well-developed ventral section of the tegulum.

The Spiral Embolus. — The spiral embolus, consisting of a truncus and a pars pendula as in *Thaumasia*, *Architis/Staberius*, and the *Pisaura* genus-group, occurs in many other spider families and is perhaps traceable in *Liphistius* [Fig. 1; *see* below under (**3**)]. In several pisaurid genera, the pars pendula is reduced and the truncus appears to be very thin, especially distally, thus producing a whip-like embolus (as in *Thalassius spinosissimus*, *Pisaurina* and the *Trechalea* genus-group).

(2) Systematic Implications

A definitive cladistic analysis of the approximately 55 pisaurid genera based on genitalic characters would be premature. Too many pisaurid genera, especially from Asia, are not known in sufficient detail and analyses of the female copulatory organs in both the *Pisaura* and the *Trechalea* genus-group are lacking. But the results obtained to date suggest the following phylogenetic conclusions:

The *Pisaura* genus-group includes at least: *Afropisaura* Blandin, 1976; *Caripetella* Strand, 1926; *Charminus* Thorell, 1899; *Cispius* Simon, 1898; *Cladycnis* Simon, 1898; *Euprosthenops* Pocock, 1897; *Euprosthenopsis* Blandin, 1974; *Maypacius* Simon, 1898; *Perenethis* L. Koch, 1878; *Pisaura*; *Pisaurellus* Roewer 1961; *Tetragonophthalma* Karsch, 1878; *Thalassiopsis* Roewer, 1955; *Vuattouxia* Blandin, 1979 (1979a); *Walrencea* Blandin, 1979 (1979a); and presumably also: *Chiasmopes* Pavesi, 1883; *Dendrolycosa* Doleschall, 1859; *Paracladycnis* Blandin, 1979 (1979a); *Phalaeops* Roewer, 1955; *Ransonia* Blandin, 1979 (1979a); *Rothus* Simon, 1898; *Tallonia* Simon, 1889. The group is characterized by the distal apophysis, thus it appears to form a well-supported monophyletic clade. Features in the female copulatory organs (Sierwald, in prep.) support this hypothesis through more synapomorphies. It would be important to study the copulatory behavior of other genera of the *Pisaura* genus-group. The copulatory behavior of *Pisaura mirabilis* is complex: the male presents a prey item to the female (Gerhardt & Kästner, 1938: 543). If similar behavioral features are found in other members of the *Pisaura*-group, they would provide additional synapomorphies.

The *Trechalea* genus-group contains presumably the nominal genera *Demolodes* Mello-Leitao, 1943; *Dossenus* Simon, 1898; *Dyrines* Simon, 1903; *Dyrinoides* Badcock, 1932; *Enna*; *Hesydrus*; *Paradossenus*; *Sisenna* Simon, 1898; *Syntrechalea*; *Trechalea*; and *Xinguisella* Mello-Leitao, 1940. The

group is well supported as a clade through the synapomorphies found in the male palp, the structure of the egg sac, and through the parental behavior. Preliminary studies on the female copulatory organs (Sierwald, unpubl.) provide further evidence. In general, this group is poorly known. *Rhoicinus* and its relative *Barrisca* Chamberlin and Ivie, 1936 (*see* Platnick, 1979), might belong to the *Trechalea* genus-group as well. The systematic position of the *Trechalea* genus-group is unknown at this point. The assignment of the genera of this group to the family Pisauridae was based on plesiomorphic characters like the eye pattern, and similarities in the general habitus and habitats (occurrence near fresh water). Thus, the *Trechalea* genus-group is certainly not the sister group of the *Pisaura* genus-group, but the latter is more closely related to the remaining nursery-web pisaurid genera.

The remaining American nursery-web Pisauridae do not represent a monophyletic group; the affinities and relationships of single members are not known at this point. *Architis* and *Staberius* surely are monophyletic. In case more *Staberius*-species are found (*Staberius* is currently monotypic) synapomorphies will have to be discovered to warrant the existence of two separate genera (*see* Platnick, 1976). These then would represent sister taxa. Otherwise, the two nominal genera *Architis* and *Staberius* would be synonyms and the nomenclatural priority will need to be established, since both genera were described by Simon in 1898. *Architis* is the only member of the American nursery-web Pisauridae that hunts on snares (Nentwig, 1985). Webs for prey capture occur in several pisaurid genera around the world, e.g., in the African *Euprosthenops* (*see* Gerhardt & Kästner, 1938: 619), in the Asian *Eurychoera* and *Polyboea* (*see* Koh, 1989: 97, 100) and others, and also in juveniles, e.g., in *Pisaurina* (*see* Carico, 1985) and *Pisaura* (*see* Lenler-Eriksen, 1969). Web types and occurrences in pisaurid genera are not been studied in sufficient detail to allow phylogenetic conclusions. But Carico (1985) pointed out that the juvenile webs of *Pisaurina* and *Pisaura*, and the web of *Architis* are strikingly similar, which could indicate relationship.

Thalassius and *Dolomedes* share a greater number of characters with each other than with any other pisaurid. Their genital bulbs, spine-pattern on the legs (Sierwald, 1987), and the hunting behavior of most of their species on the surface of the water provide additional evidence. *Dolomedes* and *Thalassius* are considered close relatives. *Tinus* and *Thaumasia* share the proximal tegular projection and a large conductor, but no other features in the bulb are synapomorphic. The female copulatory organs of both genera display similarities (Sierwald, 1989b: figs. 11-12, 13-16; *see* also Carico, 1976: figs. 18-31): in both genera the copulatory duct is long and at least in some species, complexly coiled. Additional similarities are:

habitus and color pattern (white longitudinal stripes along the lateral sides of the body), as well as the hunting on the water surface in several species of *Tinus* (Carico, 1976; Sierwald, pers. observ. in Belize, Central America) and *Thaumasia* (Sierwald, pers. observ. on Barro Colorado Island, Panama). These features could be evidence for a closer relationship of both genera.

The genus *Pisaurina* is isolated. If its sail-shaped apophysis is a homologue of the distal apophysis in the *Pisaura* genus-group, it may be a the sister taxon of the latter.

The present study shows that monophyletic units (*Pisaura* genus-group, *Trechalea* genus-group) can be found using homologous morphological elements of the male copulatory organs. These hypotheses can be tested by finding corroborating features in female copulatory organs, somatic characters and other evidence such as behavioral data (e.g., structure of the egg sac in the *Trechalea* genus-group, mating behavior in the *Pisaura* genus-group, hunting behavior in *Thalassius* and *Dolomedes*). A study of the copulatory organs in potential sister taxa of Pisauridae either among the Amaurobioidea *sensu* Forster & Wilton (1973) or Lycosoidea *sensu* Homann (1971) will provide data to test homology-concepts of palpal elements within a more inclusive taxon, i.e., at the superfamilial level.

(3) Homology of Pisaurid Palpal Elements with Those of Other Families

Hypotheses on the homology of pisaurid palpal elements with those in other families rely nearly exclusively on data furnished by other authors, either in the form of descriptions or drawings. In the course of this study, it became evident that unequivocal interpretations of drawings and descriptions can not always be achieved: actual attachment points of membranes (or hematodochae) and of apophyses, especially at the tegulum in relation to the course of the sperm duct, are not always presented clearly. Likewise, the actual limits of sclerites can not always be determined with certainty from drawings. Therefore, the following homology concepts have to be considered with caution. But certain striking morphological similarities among unrelated groups should be mentioned.

Retrolateral Tibial Apophysis. — Apophyses at the distal end of the tibia occur in many spider families[8]. Their shape and structure are often species-typical and have been figured in many taxonomic studies. The function of tibial apophyses is uncertain and not necessarily the same in all groups. One observation in *Dolomedes tenebrosus* revealed that its retrolateral apophysis arrests the expanded bulb during copula (Sierwald & Coddington, 1988). If the retrolateral tibial apophyses in the different groups are homologous, they represent a synapomorphy for a large taxon within the Araneoclada *sensu* Platnick (1977; including Araneomorphae

except Hypochiloidea and Austrochiloidea). Lehtinen (1967: 285, fig. 6) suggested such a taxon including his Amaurobiides and Zodariides, but his analysis regarding morphology and exact position of tibial apophyses in the male palp (e.g., table 8, page 310; table 29, page 351) is too vague to draw conclusions on homology/non-homology. Griswold [in press] distinguished between apophyses at different positions on the male palpal tibia, and also reached the conclusion that the retrolateral tibial apophyses may be a synapomorphy for a large taxon within the Araneoclada. A retrolateral tibial apophysis is present in *Liphistius* (Mesothelae) (*see* Platnick & Sedgwick, 1984: 3, fig. 7), but its homology with the retrolateral apophysis within Araneoclada is doubtful.

Basal and Middle Divisions of the Genital Bulb. — Subtegulum, basal hematodocha (basal division), and tegulum (middle division) are considered homologous among all spiders. The male genital bulb of *Liphistius* already contains these basic elements (Kraus, 1978; Haupt, 1983). Furthermore, subtegulum and tegulum occur in most entelegyne spider groups. Lack of tegulum and subtegulum as distinct sclerites (in certain Mygalomorphae and "haplogyne" spiders) is currently interpreted as secondary loss (either by fusion of formerly distinct sclerites or by paedomorphosis during ontogeny, *see* Coddington [in press]). The ontogenetic evidence supports this conclusion.

Subtegulum. — The pisaurid type of subtegulum with a sclerotized distal ridge and anelli occurs in other families as well (Agelenidae [Comstock, 1910: fig. 24; Gering, 1953: figs. 27, 31; *see* Bennett, 1987, for a detailed description of the subtegulum in Agelenidae], Thomisidae [Loerbrocks, 1984: fig. 9], and Phyxelidinae [Griswold, in press]). The morphological structure of the subtegulum often does not receive detailed attention in monographic studies. Details on its morphological diversity are therefore lacking.

Distal Tegular Projection. — Enlargements and elaborate structure of the distal tegular area occur in several spider groups independently. In Linyphiidae, the suprategulum corresponds in its position to the distal tegular projection as it is found in Pisauridae. The linyphiid suprategulum does not contain a loop of the sperm duct, thus the complex structure and enlargement of the distal tegular area in both families is obviously homoplasous. Griswold [in press] described an embolic sclerite (EBS) in some genera of Phyxelidinae that also corresponds to the distal tegular area.

Median Apophysis. — Haupt (1983: 276, figs. 1a-e) presented hypotheses that (a) the median apophysis is a homologue in all spiders, and (b) it can be traced back to the Kontrategulum in *Liphistius* and *Heptathela*. The Kontrategulum *sensu* Haupt is a ring-segment broken out of the ring-like tegulum in *Liphistius*. Haupt did not present any further

details on the Kontrategulum = median apophyses hypothesis (e.g., by comparing it in various families, giving morphological criteria or describing different character states of the Kontrategulum in other spiders). He only presented the araneid median apophysis as the representative for the "median apophysis" in all entelegyne spiders. Raven (1985: 15) argued convincingly that the segmentation of the tegular ring in liphistiids appears to be an autapomorphy of subunits within the group or of certain *Liphistius* species. Haupt's claim that the median apophysis of all other spiders is a derivative of the Kontrategulum of *Liphistius* is therefore unsubstantiated.

Nevertheless, Haupt's concept of the median apophysis as an old structure, and therefore homologous in a large clade within Araneoclada, appears to be valid. The median apophysis as it occurs in Pisauridae - a distinct sclerite, at a certain position on the tegulum, connected to the tegulum via an inflatable or flexible membrane - occurs in many and unrelated families (e.g., in Amaurobiidae [Griswold, in press]; in Araneidae [Coddington, in press], in Anyphaenidae [Sierwald, 1988: fig. 1]; in Lycosidae, Fig. 48). Lehtinen (1967: 285, fig. 6, and 289, table 1) placed the "origin of the median apophysis with movable joint at the base" as a synapomorphy for his Amaurobiides, thereby excluding the Araneoidea from possessing a homologue. He did not comment on the striking similarity between the araneid median apophysis with the median apophysis in Amaurobiides.

Conductor. — As mentioned before, the term conductor has been used for tegular as well as for apical apophyses. In the Linyphiidae, the term conductor was used for a structure of the apical division. Because of doubtful homology, Saaristo (1971: 465) recommended avoiding the term conductor for Linyphiidae. Another example for inconsistent use of the term conductor appears in the family Lycosidae. Whereas in most lycosid genera a tegular process is labelled conductor (e.g., *Trochosa ruricola*, Fig. 48), the membraneous "conductor" in *Pardosa* (*see* Dondale & Redner, 1984, figs. 5-7) is an apophysis of the apical division and clearly not homologous.

Haupt (1983) considered the conductor homologous in all entelegyne spiders, but did not discuss morphological and positional differences of conductors in the various groups, and thus gave no evidence for his claim. He homologized the mygalomorph conductor with the Kontrategulum. Raven (1985: 16, and fig. 11) presented convincing evidence that the mygalomorph conductor (as in *Atypus*) may be a homologue of the stiff, prominent ridges of the distal margin of the tegulum in the mesothelid *Liphistius* (*see* Fig. 1), since "the mygalomorph conductor is a sclerotized process arising opposite the embolus, separated from it by an extensive haematodocha...." Such tegular ridges occur in several *Liphistius*- and

Heptathela-species (Kraus, 1978: figs. 2-4; Platnick & Sedgwick, 1984: figs. 39, 41, 66; Haupt, 1983: figs. 4c, 7).

Lehtinen (1967: 285, fig. 6) proposed "a membraneous, secondary conductor" exclusively for Lycosoidea and Amaurobioidea *sensu* Lehtinen (including Miturgidae, Amaurobiidae, Liocranidae, Agelenidae, Dictynidae and Hahniidae). As discussed earlier, his argumentation lacks convincing morphological details to distinguish between a primary and a secondary conductor.

The pisaurid conductor as an immovable, tegular outgrowth is considered here homologous in many spider groups (e.g., Lycosidae, Anyphaenidae, Amaurobiidae, Psechridae, Araneidae). It is suggested that the basic pattern of the genital bulb in Araneoclada contains two tegular apophyses (median apophysis and conductor), as Coddington [in press] presumed as well. Coddington [in press] considered the conductor to be a homologue in Dictynoidea, Orbiculariae, and Amaurobioidea *sensu* Forster & Wilton.

Conductor and Median Apophysis. — Independent modifications, reductions or losses of one or both may have frequently occurred in various groups. If only one tegular apophysis is present, it may be difficult to identify which (the median apophysis or the conductor) has been lost. Likewise, if both are present in two not closely-related spider groups, it may be difficult or impossible to decide whether the conductor in one group is homologous to the median apophysis in the other group or vice versa. Slight changes in the growth pattern of the tegulum could result in rather different insertion points of the tegular apophyses in relation to the trajectory of the sperm duct in the mature genital bulb.

Apical Division. — In many Mygalomorphae and "haplogyne" spiders the apical division consists of the embolus, forming a mere continuation of the middle division rather than being separated from it (connate type of embolus *sensu* Comstock, 1910: 182). The mygalomorph conductor, often assigned to the apical division, appears to be a tegular apophysis, as Raven (1985) showed (*see* above). In entelegyne spiders, the apical division is often a complex structure.

Basal Membraneous Tube of Apical Division. — The large sclerites of the genital bulb are usually connected via less sclerotized, membraneous tubes, which are called hematodochae, when they are large and inflatable. The column, as described by Saaristo (1971) for Linyphiidae (called duct membrane by Merrett, 1963), connecting the tegulum and the apical division corresponds in position to the basal membraneous tube as found in Pisauridae. The character state as an inflatable, rather large membraneous tube is supposedly independently derived.

Distal Sclerotized Tube of Apical Division. — In Araneidae, the

apical division consists of two tubes with the ejaculatory duct running through them (Grasshoff, 1968: figs. 33a, b). The proximal tube, called the radix, is fully sclerotized. The second, distal tube is partly sclerotized and partly membraneous (*see* below, Stipes). A radix has been described for other spider families (e.g., Uloboridae, Oecobiidae, Theridiidae) but Coddington [in press] considered none of these homologues to the araneid radix based on major morphological differences and arguments involving parsimony. He argues that the true radix is most likely a synapomorphy for Araneidae and Linyphiidae. The distal sclerotized tube of the apical division in Pisauridae appears to be similar to the araneid radix, morphologically and positionally. A similar sclerite was described by Gering (1953: fig. 6) in *Agelenopsis*. The possible homology of these sclerotized tubes of the apical division deserves further attention.

Embolus. — A detailed study on the morphology of emboli in spiders is lacking. Whether emboli contain one or several sclerites, the shape of such sclerites, and the extent of membraneous sections are often missing in morphological descriptions. As mentioned earlier, only Comstock (1910) described different morphological types of emboli. The opening of the sperm duct always identifies the embolus itself unambiguously. But the opening of the sperm duct only identifies the terminal end of the embolus, not the proximal end of the structure.

A survey of 53 araneomorph spider families showed that spine-like emboli are most common. Comstock called these spiral emboli, consisting of a gutter-like sclerite, the truncus, and a membraneous pars pendula. Together they form a tube. The typical spiral embolus has a broad base and a tapering terminal section (e.g., in *Architis*, Fig. 42). The length of the terminal section varies. Long terminal sections may perform a loop as *Thaumasia* (Figs. 16, 17). Such loops of the terminal section occur also independently in e.g., Linyphiidae (*Lasiargus*, Whiele, 1960: fig. 21a), Theridiidae (*Achaearanea*, Levi, 1961: fig. 7), and Stiphidiidae (*Stiphidion*, Davies, 1988: fig. 23). Very long emboli often form multispiral coils as in *Tinus* (Fig. 11). Such coiled emboli are broadened and tape-like. This type occurs independently in e.g., Deinopidae (*Deinopis*, Kraus, 1956: fig. 4), Symphytognathidae (*Patu*, Forster & Platnick, 1977: fig. 53), Linyphiidae (*Labulla*, Merrett, 1963: fig. 33), Mysmenidae (*Mysmenopsis*, Gertsch, 1960: fig. 45, 46), Pacullidae (*Sabahya*, Deeleman-Reinhold, 1980: fig. 10), and Theridiidae (*Latrodectus*, Wiehle, 1960: fig. 11).

In addition to a sclerite, emboli often contain membraneous parts, especially in the basal region (e.g., Figs. 18, 23). Gering (1953: 26, figs. 29, 30; Agelenidae), Loerbrocks (1983: figs. 4, 6; Thomisidae), and Griswold (in press; Amaurobiidae) labelled membraneous parts of emboli pars pendula. Comstock (1910: fig. 6) used the term in a theraphosid

embolus, obviously implying homology. Often, membraneous sections in the base of the embolus are indicated in drawings, but not confirmed in descriptions (e.g., Senoculidae [*Senoculus*, Petrunkevitch, 1925: fig. 105], Linyphiidae [*Cornicularia*, Wiehle, 1960: fig. 10], Lycosidae [*Schizocosa*, Dondale & Redner, 1978: fig. 10; *Sosippus*, Brady: 1962, fig. 36]).

It is my current hypothesis that all spine-like emboli, containing the truncus and a pars pendula, are in fact homologous. The question is at what level are they homologous?

Since the genital bulb of Mesothelae already contains the two large sclerites, subtegulum and tegulum, the structure of its apical division is of special importance. In *Liphistius* (Fig. 1), the apical division consists of a large sclerite (sclerite III *sensu* Kraus, 1978) bearing one elongated sclerotized projection and two lamellae (bl = broad lamella and hl = hyaloid lamella; after Kraus, 1978). The sclerotized projection is U-shaped in cross section and forms three sides of the embolus. The fourth, open side is closed by the hyaloid lamella, thus forming a tube-like embolus[9]. Haupt (1979: 360) described the embolus of *Ryuthela nishihirai* (Haupt, 1979)[10] as " strongly sclerotized except for a longitudinal groove... [citation translated]," presumably describing a homologue of the hyaloid lamella *sensu* Kraus of *Liphistius*.

The resemblance of the liphistiid embolus to the "spiral type of embolus" as described above is striking. This morphological similarity could imply homology of at least the projection of the sclerite III (*sensu* Kraus) with the truncus of the spiral embolus in entelegyne spiders.

Since all emboli in spiders seem to contain a sclerite or form a sclerotized tube, I propose that it is most parsimonious to assume that the embolic sclerite in all spiders is a homologue of either the complete sclerite III or the projection of sclerite III in *Liphistius*. This hypothesis is in concordance with the homology of subtegulum and tegulum in all spiders. The pars pendula could be a homologue of the hyaloid lamella, but I am less confident of such a hypothesis. Supporting evidence for the latter hypothesis could come from ontogenetic studies of genital bulbs, or from the occurrence of membraneous sections in the emboli of Paleo- and/or Neocribellate spiders. But even then, homology may be difficult to hypothesize since a membraneous section is not complex in structure. Therefore, morphological similarity may not offer supportive evidence for homology. If the pars pendula in the emboli of entelegyne spiders is not homologous with the hyaloid lamella in *Liphistius*, the spiral embolus may be a synapomorphy for a large group within the Araneoclada *sensu* Platnick. A re-examination of the embolic area of spider groups with other types of emboli (e.g., coniform and lamelliform *sensu* Comstock) may reveal unexpected morphological similarities and may lead to new homology

concepts as the following indicates.

Stipes in Araneidae. — In addition to the proximal sclerotized tube called the radix, the apical division of some araneids contains a second, distal tube. The latter tube carries none to several terminal apophyses and an embolus. Part of the wall of the second tube is sclerotized, forming a sclerite called the stipes. The remaining part of the tube wall is membraneous and inflatable (called distal hematodocha by Grasshoff, 1968: fig. 33), carrying terminal apophyses and a short embolus. This embolus was figured by Comstock (1910: fig. 25) and called the coniform embolus. It is possible that the stipes-section of the araneid bulb is an enormously developed spiral embolus, with the stipes representing the truncus and the membraneous part representing the pars pendula, thus the distal hematodocha would be the homologue of the pars pendula. If this is true, the traditional araneid embolus corresponds only to a part of the embolus in Pisauridae and other groups with spiral emboli.

Haupt (1983) and Heimer (1986) both discussed the striking similarities in morphology of the genital bulbs in Mesothelae and entelegyne spiders. Because of the "presumed great phylogenetic distance between Araneoidea and Liphistiidae...," Heimer (1986: 119) explicitly avoided the term homologous but attributed the morphological similarity to homoiology. This term, meaning analogous structures in homologous organs, is not part of the current set of terms used in phylogenetic systematics. Although divergent definitions exist[11], the term basically means parallelism. Heimer's statement makes it difficult to recognize on what level he considers parts of the genital bulb homologous within Araneae.

As shown above in the discussion on the conductor, median apophysis, and spiral embolus, I believe that careful morphological analysis and comparison will enable us to establish homologies of palpal structures within Araneae at all taxonomic levels. This knowledge of homologous elements in the male palpal organ, as well as in the female copulatory organ, will greatly advance the reconstruction of the phylogeny of Araneae.

SUMMARY

Morphology and Homology of Palpal Elements

It is now generally accepted that the tripartite genital bulb in male spiders is plesiomorphic (genital bulb structure in Mesothelae, ontogenetic evidence; *see* Platnick & Gertsch, 1976, Kraus, 1978, and Haupt, 1983). The large sclerites (subtegulum and tegulum) are therefore homologous in all spiders.

It is proposed here that morphological similarity and position of tegular apophyses and processes often provide sufficient evidence for

homology concepts (process connected via membrane to tegulum or mere outgrowth of tegulum; process containing a loop of the sperm duct or lacking such). The basic pattern in Araneoclada *sensu* Platnick (1977) contains two tegular apophyses (median apophysis and conductor). A conductor found in the apical division (as described in e.g., Linyphiidae) is not a homologue of the true conductor.

It is suggested here that the spiral embolus *sensu* Comstock (1910) is a plesiomorphic feature and homologous for a large clade. The sclerite of the spiral embolus, the truncus, is considered to be a homologue of the projection or the entire sclerite III in the apical division of *Liphistius*. Furthermore, it is suggested that other types of emboli, e.g., the coniform embolus of Araneidae, may only be partly homologous to the spiral embolus, but that the araneid stipes may represent a homologue of the truncus. The araneid radix of the apical division is compared to the distal sclerotized tube as it occurs in the apical division of Pisauridae and possible homology is discussed.

The retrolateral tibial apophysis as it occurs in Pisauridae is homologous wherever it is found in other spider families and therefore represents a synapomorphy for a large clade within Araneoclada.

Palp Morphology of American Nursery-Web Pisauridae

Architis/Staberius, Pisaurina, Thaumasia, Tinus, and *Dolomedes* constitute the American nursery-web Pisauridae. Only *Dolomedes* is distributed worldwide, the remaining genera are restricted to the Americas. All American nursery-web Pisauridae possess a well-developed and species-typical retrolateral tibial apophysis. The subtegulum bears a sclerotized ridge and anelli. The tegulum is ring-like (bowl-like in *Pisaurina*). The distal end of the tegulum (distal tegular projection) is enlarged and contains a loop of the sperm duct.

Dolomedes possesses a membraneous conductor, the median apophysis is flat, lamelliform, and species-group specific. *Thaumasia* and *Tinus* have a large conductor, heavily sclerotized in *Tinus*; the genus-typical median apophyses are short with a slightly sclerotized distal region. The conductor is independently reduced in *Pisaurina* and *Architis/Staberius*. The median apophysis in the latter is very similar to the one found in *Tinus* and *Thaumasia*. *Pisaurina* possesses a well-developed, species-typical median apophysis and an additional, tegular, sail-shaped apophysis that is presumably a homologue of the distal apophysis as found in the *Pisaura* genus-group. *Tinus* and *Thaumasia* both possess a sclerotized, proximal, tegular process that is large in *Tinus* and short in *Thaumasia*.

The apical division of Pisauridae consists of a basal membraneous tube connected to the distal end of the tegulum, a sclerotized distal tube

and a spiral embolus *sensu* Comstock (1910). *Dolomedes* carries a terminal apophysis called the fulcrum. A homologue of the fulcrum is found in *Tinus* in form of a small club-shaped apophysis. In *Tinus*, the basal membraneous tube of the apical division is large, forming a species-typical, coiled, inflatable sac.

The bulb structure of the African genus *Thalassius* is very similar to *Dolomedes*, indicating closer relationship.

Palp Morphology of the *Pisaura* Genus-Group

The tegulum is bowl-like. The conductor is sclerotized and well developed. The conspicuous, distal tegular apophysis in addition to the median apophysis, and structure of the apical division are synapomorphies of the group. Preliminary studies of the female copulatory organ corroborate monophyly of this clade.

Palp Morphology of the *Trechalea* Genus-Group

The *Trechalea* genus-group possesses the following synapomorphies in the genital bulb: a small, reduced conductor, a median apophysis with two branches, a sperm duct with several switchbacks, a well-developed ventral section of the tegulum and a conspicuous membraneous pit at the distal end of the palpal tibia. Preliminary studies of the female copulatory organs, the structure of the egg sac and maternal behavior (attaching the egg sac to the spinnerets) corroborate the monophyly of this clade.

Systematics of the Family Pisauridae

So far, no morphological synapomorphies have been found to unite the 55 genera assigned to the family Pisauridae. An assumed apomorphy, the nursery-web, built by the female for the newly hatched spiderlings has been observed to date in nine genera belonging to all three subfamilies of Pisauridae. Thus, to define monophyletic units among pisaurid genera, morphological synapomorphies have to be found. The sister group to Pisauridae is unknown, but should be among the Lycosoidea *sensu* Homann (1971), since this superfamily is united by the synapomorphy of a grate-shaped tapetum in the secondary eyes. Lehtinen's (1967) separation of Pisauridae *sensu lato* in Dolomedidae and Pisauridae *sensu stricto*, placed in two different superfamilies, is rejected at this point. The main distinction between the two, the primary conductor in Pisauridae *sensu stricto* and the secondary conductor in Dolomedidae appears to be unsubstantiated.

Based on the structure of the genital bulb, the *Pisaura* genus-group contains at least: *Afropisaura* Blandin, 1976; *Caripetella* Strand, 1926; *Charminus* Thorell, 1899; *Cispius* Simon, 1898; *Cladycnis* Simon, 1898; *Euprosthenops* Pocock, 1897; *Euprosthenopsis* Blandin, 1974; *Maypacius* Simon, 1898; *Perenethis* L. Koch, 1878; *Pisaura* Simon, 1885; *Pisaurellus*

Roewer, 1961; *Tetragonophthalma* Karsch, 1878; *Thalassiopsis* Roewer, 1955; *Vuattouxia* Blandin, 1979 (1979a); *Walrencea* Blandin, 1979 (1979a); and perhaps also: *Chiasmopes* Pavesi, 1883; *Dendrolycosa* Doleschall, 1859; *Paracladycnis* Blandin, 1979 (1979a); *Phalaeops*, Roewer, 1955; *Ransonia* Blandin, 1979 (1979a); *Rothus* Simon, 1898; *Tallonia* Simon, 1889.

The remaining American nursery-web Pisauridae do not represent a monophyletic clade. *Tinus* F. O. Pickard-Cambridge, 1901, and *Thaumasia* Perty, 1833, are closely related to each other and that clade is related to *Dolomedes* Latreille, 1804, and *Thalassius* Simon, 1885. The affinities of *Architis* Simon, 1898, and *Staberius* Simon, 1898, are unknown. The genus *Pisaurina* Simon, 1898, is presumably most closely related to the *Pisaura* genus-group.

The *Trechalea* genus-group contains presumably the nominal genera *Demolodes* Mello-Leitao, 1943; *Dossenus* Simon, 1898; *Dyrines* Simon, 1903; *Dyrinoides* Badcock, 1932; *Enna* O. Pickard-Cambridge, 1897; *Hesydrus* Simon, 1898; *Paradossenus* F. O. Pickard-Cambridge, 1903; *Sisenna* Simon, 1898; *Syntrechalea* F. O. Pickard-Cambridge, 1902; *Trechalea* Thorell, 1870; and *Xinguisella* Mello-Leitao, 1940. Based on features in the copulatory organs of both sexes, the structure of the egg sac, and parental care, the *Trechalea* genus-group is not a close relative of the nursery-web Pisauridae.

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ENDNOTES

[1]Members of Sparassidae (e.g., *Heteropoda venatoria* Linnaeus, 1767; pers. observ.) carry the flat, discus-shaped egg sac in their chelicerae as well.

[2]The egg sac of Lycosidae is also attached to the spinnerets. Although the lycosid egg sac possesses a seam, it consists of two equally shaped and equally constructed halves, thus is significantly different from the egg sac of the *Trechalea* genus-group. Attaching the egg sac to the spinnerets occurs also in the ctenid *Cupiennius* Simon, 1891 (*see* Melchers, 1963).

[3]Processes at the subtegulum are very rare. The only ones known to me occur in *Liphistius langkawi* and *L. murphyorum* (*see* Platnick & Sedgwick, 1984: figs. 31-35, 38-42).

[4]Osterloh (1922: 333) distinguished between apophyses that arrest the bulb (Retinulum) and those which engage in the female epigynum (Retinaculum).

[5]Exception: *Thalassius* Simon, 1885, is the only member of Pisauridae with a reduced tibial apophysis (Sierwald, 1987).

[6]Roewer (1955) called the median apophysis in *Thalassius* conductor.

[7]This behavior occurs also in *Ancylometes* (*see* Merrett, 1988) and *Thalassius* (*see* Sierwald, 1989a).

[8]A superficial count of spider families with such retrolateral tibial apophyses exceeded over 20 families, including: Acanthoctenidae, Agelenidae, Amaurobiidae, Ammoxenidae, Anyphaenidae, Clubionidae, Ctenidae, Dictynidae, Gallieniellidae, Gnaphosidae, Hahniidae, Heteropodidae, Homalonychidae, Oxyopidae, Pisauridae, Philodromidae, Psechridae, Salticidae, Selenopidae, Senoculidae, Tengellidae, Thomisidae, Toxopidae, Zodariidae.

[9]Raven (1985: 15) misidentified the hyaloid lamella at the embolus of *Liphistius* as being the mesothelid conductor.

[10]*See* Song & Haupt, 1984, for the taxonomic position of *R. nishihirai.*

[11]Dzwillo, 1978: 96; Riedl, 1975: 60. Ax (1984: 63) considered the terms parallelism, homoplasy, and homoiology superfluous. Patterson (1982: 45-48) gives an enlightening analysis of the terms homology, homoiology, homonomy, parallelism, and convergence.

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